

PROCEEDINGS OF THE LINNEAN SOCIETY OF LONDON

151st Session (1938-9)

Part 2

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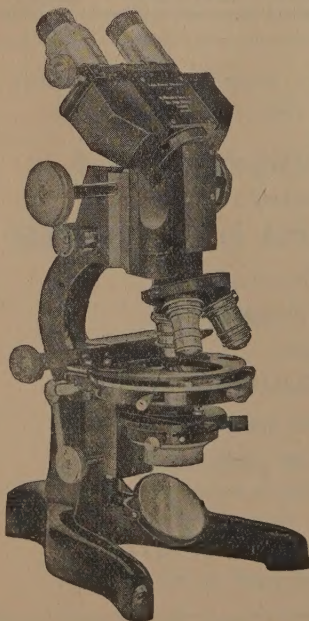
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PROCEEDINGS OF THE LINNEAN SOCIETY OF LONDON

151st Session (1938-9)

Part 2

PROCEEDINGS OF THE GENERAL MEETING

5 January 1939

MR. J. RAMSBOTTOM, O.B.E., M.A., Dr.Sc., President,
in the Chair

The Proceedings of the General Meeting held on Thursday 8 December 1938, having been circulated were taken as read and confirmed.

The President announced that a fund was being raised to repair the monument to PHILIP MILLER (1691-1771) in Chelsea Old Church yard, to which the Royal Horticultural Society, the Apothecaries Company, and the Chelsea Society had already made donations; and it is proposed that Fellows of the Society who wished to do so should contribute a collective donation amounting to £10.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

The following Fellow signed the Obligation in the Book of the Charter and Bye-Laws and was admitted:—The Rt. Rev. Arthur Cayley Headlam, Bishop of Gloucester.

Certificates of recommendation of the following candidates for Fellowship were read:—For the second time, in favour of Clarice Vivian; for the first time, in favour of John Frederick Gustav Chapple and Leonard Richmond Wheeler.

The President reported the deaths of the Abbé Victor Grégoire, F.M.L.S., and Major H. A. Cummins, C.M.G., F.L.S.

Prof. T. G. B. OSBORN, F.L.S., and Mr. C. A. GARDNER (Visitor) gave a joint-account of 'Dampier's Australian plants', and exhibited some of the original specimens. [Printed in full below, p. 44.]

Dr. F. W. JANE, F.L.S., and Miss R. E. DOWLING, F.L.S., gave a joint-account, 'On the occurrence of *Mastigosphaera Gobii* Schewiakoff in Britain'. [Printed in full below, p. 50.]

Mr. C. R. STONOR (Visitor) gave an account, illustrated by specimens, of 'Some interesting Birds from New Zealand'.

Abstract.—

The isolation of New Zealand is very ancient, and, considering the favourable nature of natural conditions for birds, the number of resident species is very small.

There are many very remarkable types, excluding the extinct Moas, whose nearest relative is the Kiwi. The ducks are represented by several species, one of the most interesting of which is the Paradise Duck, whose plumages and breeding behaviour both call for comment. The Waders include the Black Stilt (a mutant from the White-headed species), a Dotterel, and the Wrybill.

The Parrots are among the most remarkable forms; and the most striking species is the Owl-Parrot, a nocturnal, flightless species, with unusual breeding habits. Other New Zealand Parrots are the Kea and the Kaka.

The Passerine birds are represented by the Tui or Parson-bird, the White-eye which has colonized New Zealand from Australia, and many others. Particularly remarkable are the Crow-like birds, the Wattled Crow, the Saddleback, and the now extinct Huia.

An interesting history is that of the Stephen Island Wren, exterminated by a single cat.

Mr. I. HENRY BURKILL, Sec.L.S., gave an account of his paper, 'Two notes on *Dioscoreas* in the Congo: (1) The *Acarodomatia* of *D. minutiflora* Engl. and *D. smilacifolia* De Wild.; (2) Twining in both directions in *D. Baya* De Wild.'. [Printed in full below, p. 57.]

DAMPIER'S AUSTRALIAN PLANTS.

By Prof. T. G. B. OSBORN, F.L.S., and Mr. C. A. GARDNER.

FROM time to time references occur in the literature to a small collection of about forty plants reputed to have been made in 1699 on the coast of New Holland by the buccaneer and navigator William Dampier. These are part of the Sherardian Herbarium, Department of Botany, Oxford. No description of the collection has been given by any botanist familiar

with the Australian flora. It was not made available to Bentham when writing the 'Flora Australiensis', although von Mueller had inquired about its contents. This is probably because M. A. Lawson, then Sherardian Professor, dismissed it as having 'no particular points of interest'. (Journ. Bot. xi, p. 348; 1873.) This is far from being the case. It contains one of the specimens on which Robert Brown formed the curious Rutaceous genus, *Diplolaena*, and the cotype of his species, *Dampiera incana*. Moreover, it has an historic interest. It contains the plants of *Terra Australis Incognita* which impressed the first Englishman who has left any record of his visit to those shores—71 years before Sir Joseph Banks landed with Captain Cook at Botany Bay.

Two points about the collection should be remembered in criticizing its contents. Firstly; Dampier was not a botanist. He appears to have picked either plants which were peculiar or strange to him, e.g. *Clianthus* and *Dampiera*, or plants which looked familiar, e.g. 'Rosemary' and grasses. He probably had not thought of making a complete collection, e.g. he did not bring a specimen of Mulga, *Acacia aneura*, probably the most characteristic tree in this part of Australia. Many of the specimens are mere scraps. Secondly; he visited, during the dry season of the year, only a few places on the coastal strip of one of the driest parts of Australia and the region of least rainfall reliability—an area which never bears a rich flora, though some rain must have fallen not long before his visit, since he collected the two grasses and the ephemeral *Trachymene*.

History of the Collection.—Dampier, in command of H.M.S. *Roebuck*, cruised along the NW. coast of Australia from Shark Bay to the Dampier Archipelago between 6 August and 'early September', 1699. On the outward voyage he had spent about a month at Bahia, Brazil. After leaving Australia he visited Timor, sailed along the north coast of New Guinea, rounded New Britain which he discovered to be an island, and so to Batavia. There he refitted for the voyage home. He was unfortunate, for the ship 'foundered through perfect age' off Ascension Island. Whether all the plants were saved we can never know. Dampier did not make many landings on the New Holland Coast nor did he spend long ashore according to the account in his book, 'A Voyage to Australia' (1703, and cited below as 'Voyages, III'). He was concerned to find water. Actually he seems to have spent more time on land during a previous visit, 4 January to 5 March 1688, with a party of buccaneers. There is no evidence that he collected any plants then.

Dampier states in his preface that he had a draughtsman

with him on the *Roebuck*, which may account for the quality of the figures in his book. He also says that 'the plants themselves are in the hands of the ingenious Dr. Woodward'. Woodward is sometimes credited with the authorship of the descriptions given in *Voyages*, III, pp. 155-61. Actually he seems to have done little more than translate Ray's descriptions ('*Historia Plantarum*', III, Appendix, pp. 225-6) then in the press. Woodward also gave six other specimens to Plukenet, who described and figured them in his '*Amaltheum Botanicum*'. It appears that nothing was done with the remainder. However, sooner or later, William Sherard acquired the greater part of the material for his herbarium. It was he who sent the specimens to Ray. Sherard may even have acquired the entire collection, but two of the plants described by Ray and three described by Plukenet are missing.

Sherard's Herbarium was contained in several large volumes in which he, Dillenius, John Sibthorp, and others added descriptions or notes. These books were cut up and the specimens, together with the relevant notes, mounted on standard sheets under the instructions of Sir Isaac Bayley Balfour when Sherardian Professor (1884-1887). Each specimen was then given a running number, which is that cited below. The 'Dampier Collection' was numbered 1 to 40. Hooker (*Introd. Essay Fl. Tasm.*, p. cxiii) had said in 1860, on the authority of Baxter, then Curator of the Oxford Botanic Garden, that there were forty specimens. But this was inaccurate. Of the forty specimens attributed to Dampier there is no evidence that six were collected by him. Of the thirty-four authentic specimens, seventeen came from New Holland, the remainder from Brazil, Timor, or localities unknown.

List of the Plants.—The evidence that any one of the specimens mentioned below was collected by Dampier is derived in one or more of the following ways:—

- (a) It is labelled in Sherard's handwriting with the name given in *Voyages*, III, usually with a reference to the plate and figure. By this means it is possible to recognize the actual specimen.
- (b) It is labelled in Sherard's handwriting with a similar reference to Plukenet's '*Amaltheum Botanicum*'. Plukenet's figures, however, are not so accurately drawn as those in *Voyages*, III, so that it is not possible to identify the actual specimen with certainty.
- (c) It bears the single word 'Dampier' in Sherard's handwriting. In this case there is, of course, no locality, but it is not very difficult to recognize those plants which are Australian from those from elsewhere.

- Paractaenum novae-hollandiae* Beauv. Herb. Sherard, 19.
A single leaf and inflorescence.
- Plectrachne* sp. (aff. *Triraphis bromoides* F. Muell.). Herb. Sherard, 20.
- Grevillea* sp., probably *G. pyramidalis* A. Cunn. ex R. Br. Herb. Sherard, 22. Small shoot with leaves only.
- Pittosporum phylliroides* DC. Herb. Sherard, 27. Two small shoots, one with flowers and the broad rather revolute leaves of the NW. Australian form.
- Acacia rostellifera* Benth. Herb. Sherard, 38. Labelled '*Chamaelea arabum folio, fructu ex alis foliorum pediculis brevibus glomerato, ex Nova Hollandia*. Pluk. Amalth. App. Tab. 450, f. 7'. Four small shoots with unopened flowers, one possibly that figured.
- Clianthus speciosus* (G. Don) Aschers. & Graebn. Herb. Sherard, 15. Labelled '*Colutea Novae Hollandiae, fl. amplis coccineis, umbellatim dispositis, macula purpurea notatis*. Dampier *Voiaga* vol. 3, Tab. 4, fig. 2. *An coral arboris species*'. Several detached blooms and two inflorescences, one of which is figured by Dampier. No leaves.
- ? *Tephrosia* sp. Herb. Sherard, 31. A mere scrap with unopened flower buds, probably referable to this genus.
- Aeschynomene indica* Linn. Herb. Sherard, 28. A good specimen with flowers and unripe fruit.
- Diplolaena Dampieri* Desf. Herb. Sherard, 8. Labelled '*Dampier Voiaga, vol. 3, Tab. 3, fig. 3*'. Two inflorescences; one attached to a small shoot with leaves, being that figured by Dampier. Robert Brown refers to this specimen in his comment upon this remarkable genus of the Rutaceae (Misc. Bot. Works, I, p. 17; 1866). Desfontaines recognized from the figure that his new species was the same as Dampier's plant.
- Sida calyxhymenia* J. Gay. Herb. Sherard, no number. Labelled '*Alcea novae Hollandiae foliis angustis, utrinque villosis*. Dampier *Voiaga, vol. 3, Tab. 3, fig. 2*'. The figured specimen.
- Hannafordia quadrivalvis* F. Muell. Herb. Sherard, 6. Labelled '*Ricinoides Novae Hollandiae, anguloso, crasso folio*. Dampier *Voiaga, vol. 3, Tab. 2, fig. 3*'. The figured specimen.
- Frankenia pauciflora* DC. Herb. Sherard, 34. Several pieces, some with fruits. Identified by Mr. V. S. Summerhayes as 'very similar to the type variety'.
- Beaufortia Dampieri* A. Cunn. Herb. Sherard, 10. The label in Sherard's writing reads, '*Dammara ex Nova Hollandia, sanamundae secundae Clusiis foliis*. Dampier *Voiaga,*

vol. 3, Tab. 3, fig. 4. *Raj. Hist.* III, app. 225'. The specimen is that figured by Dampier*. A. Cunningham (Bot. Mag. 60, no. 3272; 1833) recognized that his *Beaufortia* was *Dammara ex Nova Hollandia*.

Didiscus pusillus (DC.) F. Muell. Herb. Sherard, 23. Labelled 'Umbelliferae adfinis, Ranunculi folio, planta pusilla, Hollandiae Novae. Pluk. Amalth. Append. Tab. 454, fig. 6'. The specimen is possibly that figured, but it cannot be identified with certainty.

Solanum orbiculatum Dun. Herb. Sherard, 7. Labelled 'Solanum spinosum Novae Hollandiae Phyllifoliis subrotundis. Dampier *Voiaga*, vol. 3, Tab. 2, fig. 4'. Two small specimens, the larger being that figured.

Myoporum acuminatum R. Br. Herb. Sherard 37. Three small shoots with unopened flower-buds.

Dampiera incana R. Br. Herb. Sherard, 24. Labelled 'Leucoium maritimum Nov. Hollandicum, fol. parva, incano, fl. amplo, caeruleo. Pluk. Amalth. App. Tab. 452, fig. 4'. Plukenet's figure is probably a portion of this, but it is badly drawn and shows a four-lobed corolla.

In the Herbarium of the British Museum there is a small bit of an inflorescence with two opened flowers and three buds. It is said to have been collected by Dampier, and has every appearance of being from the same collection as Sherard's specimen. Probably it was given to Robert Brown when he examined the Sherardian Herbarium. From the citation given by Brown (*Prodromus*, p. 588) this must be the type-specimen. The Oxford specimen, of which there is ample material, vegetative as well as floral, would be the co-type.

Excluded specimens.—Ray (*Hist.* III, Append.) described certain other plants as collected by Dampier in New Holland. Sherard's Herbarium contains two of these, both recognizable as the figured specimens. One (Herb. Sherard, 4), labelled

* Three specimens in Sherard's herbarium are valuable as showing how the mistake arose which credited the flora of NW. Australia with a *Dammara*. They are: (a) No. 9. Labelled 'Arbor Javanensis, Visci foliis latioribus, conjugatis, *Dammara alba dicta*'. The name is Ray's ('*Historia Plantarum*', III, Dendr. p. 130). It is a sterile shoot of *Agathis alba*, about 18 cm. long. There is no evidence that Dampier collected this specimen. (b) No. 12. Labelled 'Arbor hortensis Javanorum, foliis visci angustioribus aromaticus, floribus spicatis stamineis lutescentibus. Mus. Pet. 350'. The specimen is a fruiting shoot of *Melaleuca Leucadendron*, the leaves of which are somewhat like those of *Agathis*. There is no evidence that Dampier collected this specimen. (c) No. 10, the *Beaufortia Dampieri* mentioned above. This has fruits which are obviously of the same type as *Melaleuca Leucadendron*, which, because of a superficial resemblance of the leaves, had been related to *Dammara* (i.e. *Agathis*). The comments on pp. 158-9 of *Voyages*, III, are a translation of Ray, *Historia*, III, Appendix, p. 225.

'*Rapuntium Novae Hollandiae*, fl. magno coccinio, Dampier *Voiaga*, vol. 3, Tab. 2, fig. 1' is *Centropogon surinamensis*, Presl. It is a tropical South American species and must have been collected on the outward voyage.

The second, Herb. Sherard, 14, is a sterile shoot of *Casuarina equisetifolia*. It is labelled '*Equisetum Novae Hollandiae frutescens, foliis longissimis*. Dampier *Voiaga*, vol. 3, Tab. 4, fig. 1. An *Dammara* species?' *C. equisetifolia* has not been found by any collector on the NW. Australian coast. One of us has made a careful search for it from Shark Bay to Dampier's Archipelago, but without success. Its nearest reputed locality is Cambridge Gulf, which is much further north, and east of any landing made by Dampier, though we do not know any actual specimens collected west of the Northern Territory boundary. On the other hand, as he visited Timor, New Guinea, and other places in the East Indies after leaving the Australian coast, the specimen might well have been collected elsewhere.

Missing specimens.—Two of the plants described by Ray as being from New Holland and figured by Dampier are not in Sherard's Herbarium. The numbering does not suggest that they have been lost subsequent to the time when the books were cut up, if indeed they ever were in the collection. They must have been in Sherard's possession at one time, for Ray says that the Dampier plants were sent to him by Sherard. One, *Scabiosa* (forte) *Novae Hollandiae* (Voyages, III, pl. 3, fig. 1) is probably *Conostylis candicans*, Endl. var. *leptophylla*. The description, and the figure showing a bract halfway up the scape make this identification probable. It is not uncommon on the NW. Australian coast. The other, *Conyza Novae Hollandiae* (Voyages, III, pl. 4, fig. 3) is Dampier's 'Rosemary', after which he named the island which is still so called. It is almost certainly *Olearia axillaris* F. Muell. Cunningham collected it in Dampier's archipelago.

Three of the six species described by Plukenet are not in the herbarium. One, *Chrysanthemum exiguum* Nov' *Hollandicum* (pl. 450, fig. 10) might be a species of *Brachycome*. A second, *Erica* Nov' *Hollandica quaterno ordine foliata* appears on the plate (pl. 451, fig. 4) with another name, *Erica aromatica Dammara Rumphio*. It might be a badly drawn specimen of *Beaufortia Dampieri* without the fruits. The mention of *Dammara* in the second name makes this possible. Finally, we consider it improbable that the specimen figured on pl. 453, fig. 2 was obtained in Australia.

Discussion.—

Mr. C. A. GARDNER said that the flora of the area visited by Dampier is the poorest of any of Australia's plant

formations, and is markedly xerophilous. It is doubtful if the species of the region exceed seven hundred in number.

Only at Shark Bay itself, where the South-Western Australian Province rubs shoulders with the Eremaea, do we find any richness of the flora, and here there are many very important endemics.

It is the presence of these endemics which enables us to be certain that Dampier did collect at Shark Bay.

The PRESIDENT said that Professor Osborn was to be congratulated on having traced out the historically important Australian plants collected by Dampier. The collection was not perhaps botanically important, but the specimens were in good condition and though 'scrappy' according to modern ideas were sufficient for their purpose. Dampier was obviously interested in botany, but the 'skill'd person' in the ship who drew the plants from which the figures illustrating the voyage were copied was certainly not engaged as a botanical artist.

Two of the volumes of the Sloane Herbarium (H.S. 93 & 94) containing plants from Plukenet mention on their title-pages Dampier's name among others as contributing 'plants from the East and West Indies'. However, only two flowerless shoots in H.S. 94 have so far been definitely attributed to him.

It would be of great interest to find out in detail the history of the Australian collection after it reached this country. It was a stirring thought that this small collection which they were now privileged to see had interested John Woodward, Ray, Plukenet, William Sherard, and Robert Brown.

Sir ARTHUR W. HILL also spoke.

Prof. OSBORN replied.

ON THE OCCURRENCE OF *MASTIGOSPHAERA GOBII* SCHEWIAKOFF, IN BRITAIN.

By Dr. FRANK W. JANE, F.L.S., and
Miss RUBY E. DOWLING, F.L.S.

MASTIGOSPHAERA is a monotypic genus, outstanding among the Volvocales in that its cells are uniflagellate. *M. Gobii* was found by Schewiakoff in a marsh in New Zealand some forty years ago, and was described by him in 1893. According to Pascher (1927), it has not been found in Europe, and, so far as we are aware, *Mastigosphaera* has not been seen, or at least recognized and recorded, since it was first described.

In early May 1938 a flagellate which seemed almost identical with *M. Gobii* was observed in a sample of water from a small pond in North Yorkshire, near Winston, Co. Durham; it

soon disappeared, but was found again, somewhat sparingly, in a temporary pool in the same locality in November 1938; it was still present in mid-December, which was the last occasion on which we were able to examine dippings from this pool. There can be little doubt that this flagellate is identical with that described by Schewiakoff, and as certain details—and one, at least, of a somewhat puzzling nature—have been observed, which are not mentioned by Schewiakoff, it seems desirable that a new account of this interesting organism should be placed on record.

The coenobia might well be passed over as small *Pandorina* or even *Eudorina*, and it is not improbable that this has happened in the past and that the apparent rarity of *Mastigosphaera* is, in some measure, attributable to this cause. At the same time it is difficult to believe that *Mastigosphaera* has always been overlooked owing to casual observation; we are of the opinion that it is a rare organism, although perhaps not so rare as might be inferred from the records. Once the coenobia have been studied it is not difficult to recognize them, even under a moderate magnification, and without reference to the flagella, both by reason of their small size—although *Pandorina* is sometimes no larger—and on the spacing of the cells; in *Mastigosphaera* adjacent cells touch one another, but are not flattened at their points of contact, as in *Pandorina*; spherical coenobia in fact, somewhat resemble a small motile *Coelastrum*, and in addition they tend to be of a slightly yellowish-green, rather than a grass-green colour, although this colour difference cannot be regarded as a prominent feature.

Schewiakoff described the coenobia as spherical and consisting of sixteen cells; coenobia with about sixteen cells are common, as are those composed of about thirty-two cells; less commonly eight-celled coenobia are seen and we have indirect evidence that four-celled coenobia occur; not uncommonly the organism consists of some twenty-four cells, and this, and the occurrence of other numbers not a power of two, suggests some irregularity in the divisions of the mother-cell when such coenobia are formed. The cells are surrounded by a thick mass of transparent, colourless mucilage, and the coenobia are either spherical or ellipsoidal in shape; the latter are regarded as young colonies.

The individual cells are roughly cuneate in optical section (fig. 1 D, E), being rather narrow and rounded posteriorly, while the broader anterior end is flattened, although it often rises to a slight papilla centrally, at the point from which the flagellum arises. Schewiakoff was of the opinion that there was no cell-wall, and while this cannot be observed directly the reproductive stages leave little doubt that the cells are

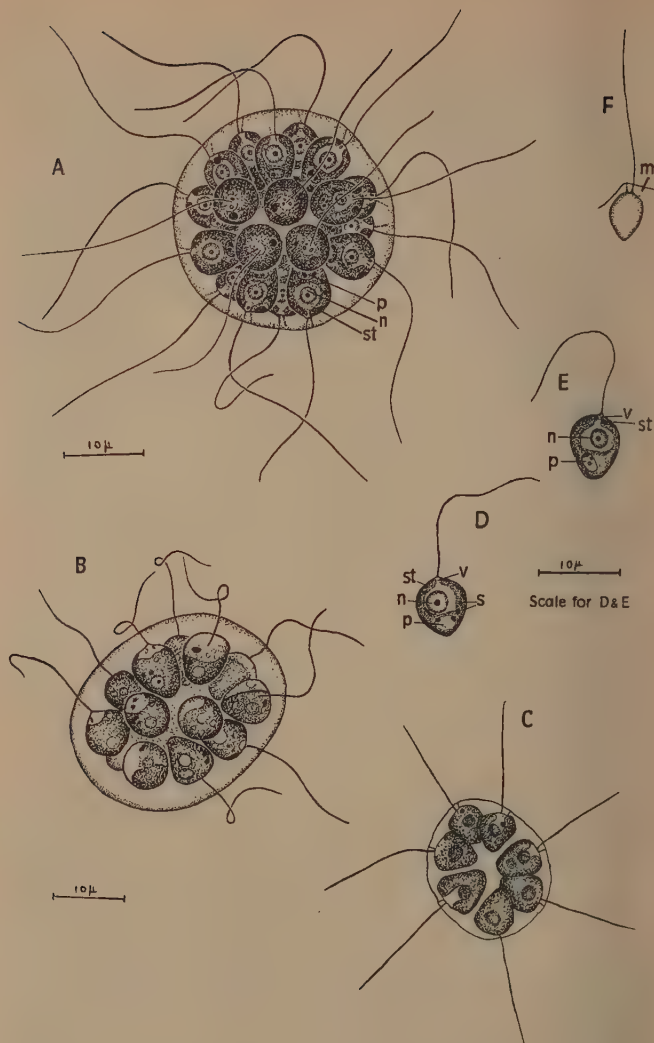


FIG. 1.—A. Coenobium of about 24 cells. (Cell-walls drawn from a specimen, but cell-contents added subsequently.) B. Coenobium in which cells have long flagella only. C. Coenobium in which cells possess 'short flagella' as well as long ones. (Scale slightly smaller than that of B.) D, E. Single cells. F. Single cell, drawn from coenobium in which mucilage had shrunk except where it was supported by the 'short flagellum'. *m*, mucilage; *n*, nucleus; *p*, pyrenoid; *s*, starch?; *st*, stigma; *v*, vacuole.

walled. The cell may be described as typically chlamydomonadine in structure, although it would be rash to generalize on minutiae of structure, both on account of the small size of the cells, which are some $8-9\mu$ long by some $5-6\mu$ broad, and also because the cells, viewed in the most favourable position (longitudinal), must be studied through a relatively great thickness of mucilage and with their posterior ends overlain by other cells. Sometimes a cup-shaped chloroplast with a massive basal region may be seen, but at other times the chlorophyll seems to be more generally distributed over the cytoplasm, and not to be confined to a cup-shaped zone. The somewhat yellowish-green colour of the chlorophyll has already been noted, but it should be emphasized that this is not a conspicuous feature. The nucleus is of the usual type, relatively large and with a well-marked nucleolus. Each cell contains a prominent eye-spot, situated anteriorly, just to one side of the point of origin of the flagellum: this stigma is approximately hemispherical, with the flattened side outermost. Schewiakoff found the pyrenoid lying somewhat anteriorly and laterally, but in our material it was always basal: in cells treated with iodine in potassium iodide a few dark specks could be seen associated with the pyrenoid, while similar specks occurred in the chloroplast; these were probably starch-grains, although their extreme minuteness rendered their exact identification uncertain. In a few cells two minute vacuoles were observed, lying anteriorly, just below the base of the flagellum; in other cells there appeared to be only a single median vacuole. On the question of vacuoles Schewiakoff is not clear; his description implies that there are two, one on either side of the flagellum base, but it implies equally that there are eye-spots in the same position; his figures suggest that there is a single vacuole, just to one side of the base of the flagellum, while the stigma occupies a similar position on the opposite side. Pascher (1927) states that there are two vacuoles.

The flagella, perhaps, constitute the most interesting feature in *Mastigosphaera*. Coenobia are frequently observed in which each cell has a single long flagellum, some three to four times as long as the cell (fig. 1 B). Often, however, the cells, or at least some of the cells of a coenobium, possess a second structure, which, for convenience, is referred to as the short flagellum (fig. 1 A, C); this is short, reaching only to the periphery of the mucilage, and does not move; it arises slightly to one side of the long flagellum. Considerable attention has been devoted to this structure: the possibility that the short flagellum is due to some shadow effect is vitiated by the fact that it remains when the coenobium rotates—in other words, as the angle of illumination changes; it has

not been confused with the tip of a flagellum of another cell, since on occasion the flagella (long and short) have been traced down to their points of origin in cells viewed from the anterior end; further, fig. 1 F shows a cell from a coenobium in which the mucilage had shrunk, although it had been held more or less in its original position in one place by the short flagellum. There is not the least doubt that the uniflagellate and heterokontan types are one and the same species, for both types of cell have been observed in daughter coenobia still within the mucilage of the mother coenobium (fig. 2 C).

Such a marked inequality of the flagella would seem to be unique in the Volvocales, although the two flagella of *Heteromastix angulata* Korsch. (the Volvocalean affinities of which are not certainly established) differ slightly in length. It might be suggested that in *Heteromastix* the second flagellum, typical of so many members of the Volvocales, is in the process of disappearing, and that in *Mastigosphaera* the process has gone farther, so that at times the second flagellum, or rather its remains, are present, sometimes not; one objection to such a view is that sister coenobia may show either condition. A more tenable hypothesis, suggested to us by Mr. D. J. Scourfield, is that the shorter flagellum, so-called, actually represents a tube in the mucilage through which the second flagellum originally passed. Whether such a tube might be expected to remain after its flagellum had disappeared is a moot point, and it might be objected that such a tube would be unlikely to support the mucilage as it lost water (cf. fig. 1 F), although the mucilage forming the wall of such a tube might conceivably be of firmer consistency than the remainder. Alternatively it may be held that the shorter structure, which for convenience has been referred to as a flagellum, is not in fact a flagellum, but a pseudocilium. This is the view towards which we incline. It is well known that pseudocilia are often difficult to see and that staining is usually necessary to demonstrate their presence in the Tetrasteraceae. Without intending to suggest that pseudocilia, if not visible, are absent, it does seem to be tacitly assumed that in genera like *Tetraspora* pseudocilia are invariably present, whether visible or not. In *Mastigosphaera* we are of the opinion that the pseudocilium, if such it be, may or may not be present, and in support of this view it may be noted that in some specimens, when stained with gentian violet—a stain used for demonstrating pseudocilia,—this structure is clearly demonstrable, while in others it cannot be seen.

Although no trace of sexual reproduction has been observed, mucilage of mother coenobia, containing daughter coenobia, has been encountered. This closely resembles the similar stage in *Pandorina* and *Eudorina*, each daughter coenobium

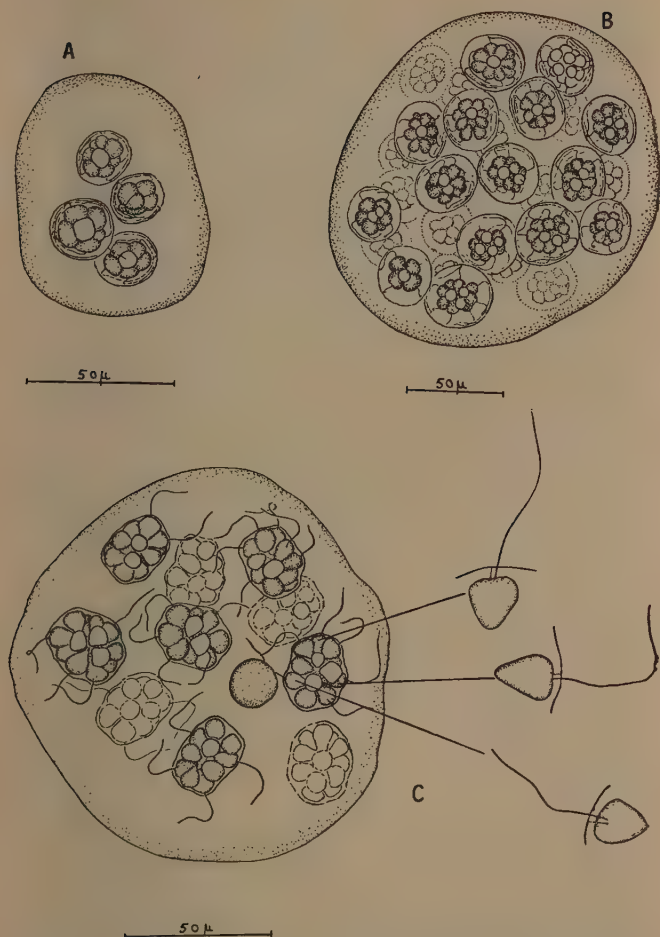


FIG. 2.—Asexual reproduction. A. Four daughter coenobia in mother mucilage. B. Twenty-eight daughter coenobia in mother mucilage. In both A and B flagella are still within the wall of mother-cell and show geniculate bend. C. Ten daughter coenobia and one undivided mother-cell in mother mucilage, flagella are free from the walls of mother-cells, but some still show geniculate bend.

being enclosed in a sac which no doubt is the remains of the wall of the mother-cell; the daughter coenobia are ellipsoidal (fig. 2), while the mother mucilage is generally spherical, evidence that the spherical coenobia represent a more mature stage than ellipsoidal ones. In this connexion it is of interest to note that Rich and Pocock (1933) note a lengthening of the polar axis with age in certain species of *Volvox*, so that in these instances the coenobia become more ellipsoidal as they become older. As few as four daughter coenobia have been observed within the mother mucilage (fig. 2 A), eight coenobia are not infrequent, while higher numbers are more common. The long flagellum of the daughter cells usually runs out to the bounding wall of the mother-cell, and is then sharply bent (fig. 2 B), and this early flexure of the flagellum would seem to be sometimes retained, as a geniculate bend often characterizes the flagella of more mature coenobia (fig. 1). The liberation of the flagella in young daughter coenobia is probably due to the wall of the mother-cell becoming mucilaginous, and contributing, in part at least, to the mucilage which surrounds the daughter coenobium.

As to the systematic position of *Mastigosphaera*, the authors are in full agreement with Schewiakoff in regarding the genus as related to *Pandorina*. But for the peculiar flagella, no doubt would be placed on its Volvocalean nature, which is confirmed by the method of asexual reproduction, a phenomenon which Schewiakoff was not fortunate enough to observe. Although the flagella would appear to be unique among the Volvocales, *Mastigosphaera* is not unique in not possessing two or four equal flagella; *Heteromastix* has already been noted, and *Polyblepharides*, *Pocillomonas*, and *Trichloris* may be mentioned as Volvocalean genera in which the number of flagella is unusual, while in *Pedinomonas* (which is not indisputably a Volvocalean genus) there is a single flagellum.

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xli, p. 8.

Mr. D. J. SCOURFIELD suggested that the appearance of a very short rudimentary second flagellum in *Mastigosphaera* might possibly be due to the existence of a tubular structure in the gelatinous coating similar to what could often be seen in *Eudorina*, and sometimes also in *Volvox*, surrounding the basal part of each flagellum. As regards the presence of only

one flagellum, he had seen one case among the Volvocales in which, immediately after division, the new individuals only had a single flagellum. Although this was presumably not the explanation of the absence of one of the flagella in *Mastigosphaera* it might give the clue to the origin of a uniflagellate species in a normally biflagellate group.

Dr. A. R. CLAPHAM (Visitor) asked Dr. Jane if he had ascertained the type of flagellum present in *Mastigosphaera*, using the Fischer technique. Three facts had impressed him as leaving open to some doubt the placing of *Mastigosphaera* in the Volvocales—the single flagellum, the failure certainly to detect starch, and the yellow-green colour. If the single flagellum should prove to be of a different type from the pair ordinarily found in Volvocales, the weight of evidence would be in favour of placing *Mastigosphaera* in some other class of Algae.

Dr. JANE replied :—

To Dr. Clapham. (1) No attempt has been made to determine if the long flagellum was of the 'Flimmer' or the Whip type. (2) It was very doubtful whether *Mastigosphaera* might be more correctly assigned to the Xanthophyceae than to the Volvocales. The flagella were a point in favour of such a course, as was, possibly, the slightly yellowish-green colour; but the organization of the cell, and in particular the chloroplast and basal pyrenoid suggested Volvocalean affinities, and this was confirmed by the method of asexual reproduction, which was identical with that of *Pandorina* and *Eudorina*. While the minute dimensions of the granules in the chloroplast precluded their certain identification, it was probable that starch was the storage product.

To Mr. Scourfield. Mr. Scourfield's suggestion that the 'short flagellum' might represent a tube in the mucilage, through which a second flagellum originally passed, was of considerable interest. It raised the question as to whether mucilage could be held in its original position in the region of such a channel, when the surrounding mucilage had shrunk owing to loss of water.

TWO NOTES ON DIOSCOREAS IN THE CONGO: (1) THE ACARODOMATIA OF *D. MINUTIFLORA* ENGL. AND *D. SMILACIFOLIA* DE WILD., AND (2) TWINING IN BOTH DIRECTIONS IN *D. BAYA* DE WILD.

By Mr. I. H. BURKILL, Sec.L.S.

THESE notes originated in a study of the rich collections of Congo plants conserved in the herbarium of the National Botanic Garden, Brussels. To Professor Walter Robyns

I tender my most sincere thanks for the opportunity of working through them.

1. The Acarodomatia of *D. minutiflora* and *D. smilacifolia*.

In the year 1903 Penzig and Chiabrera made a statement (Contributo alla cognoscenza della piante acarofile, p. 5) that acarodomatia were not known to occur in the Monocotyledones: in the next year De Wildeman rejoined that he had found them in the genus *Dioscorea* (Comptes-rend. Acad. Paris, vol. 139, p. 551) and cited two species, his own



Acarodomatia of *Dioscorea*: c, the covering margin; p, the pit between the margin and a curved nerve. Fig. 1, on *D. minutiflora*, a specimen collected by Reygaert (no. 317) used in defining *D. acarophyta*, $\times \frac{1}{2}$. Fig. 2, on *D. smilacifolia*, a specimen collected by Zenker and named *D. minutiflora* var. *Zenkeri* Uline, $\times \frac{1}{2}$. Fig. 3, on a specimen which may be regarded as *D. praehensilis* (Deighton no. 2872 from Sierra Leone), $\times \frac{1}{2}$. Fig. 4 on *D. minutiflora*, a specimen named 'balatadi' used in defining *D. armata*, $\times 1\frac{1}{2}$. Fig. 5, on *D. Pynaertii*, $\times 1\frac{1}{2}$.

D. smilacifolia and a second which he then described as *D. acarophyta*. He had described *D. smilacifolia* five years earlier, but the acarodomatia had not been mentioned, though they are present on the type-specimens (Dewèvre, 1161).

It is admitted that a connexion of Acari with these domatia has not been demonstrated, but it is convenient for continuity still to call the structures, here figured, by the name acar-

domatia. They consist of three parts: (i) a shallow pit or gallery, *p*, in the lower surface of the leaf close to the base, bordered on one side by (ii) a slightly crested nerve and imperfectly covered on the other by (iii) the margin of the leaf, *c*, which is inrolled and curiously toothed.

Eight and ten years after the date when De Wildeman called attention to these he described further species of *Dioscorea* in which they occur:—thus he described in 1912 *D. brevispicata*, *D. ealensis*, *D. echinulata*, *D. Flamignii*, *D. Lilela*, and *D. Pynaertii*; and in 1914 *D. armata*, *D. Ekolo*, *D. Engbo*, and *D. pynaertioides*. He stated of all except *D. Lilela* that the leaves carry acarodomatia; and I have verified that all do. He added also that *D. minutiflora* var. *Zenkeri* Uline, obtained in the Cameroons, carries them. He figured *D. ealensis* (Ann. Mus. Congo, ser. 5, III, pl. 55) in a plate in which their presence can be detected, and *D. echinulata* (pl. 56) with their presence obvious, and *D. Pynaertii* (pl. 65) with them just indicated.

His list of Congo *Dioscoreas* possessing acarodomatia thus becomes imposing, but a critical examination of the material leads to a reduction of them to three. I do not say that there are not differences between the specimens on which the thirteen species are based; but the differences are not specific. I find that the synonyms should be distributed thus:—

<i>D. minutiflora.</i>	<i>D. smilacifolia.</i>	<i>D. Pynaertii.</i>
<i>D. acarophyta.</i>	<i>D. echinulata.</i>	(It is possible to regard this as a large-fruited var. of <i>D. minutiflora</i> .)
<i>D. armata.</i>	<i>D. Flamignii.</i>	
<i>D. brevispicata.</i>	<i>D. minutiflora</i>	
<i>D. ealensis.</i>	var. <i>Zenkeri.</i>	
<i>D. Ekolo.</i>		
<i>D. Engbo</i> (unless it is <i>D. Pynaertii</i>).		
<i>D. Lilela.</i>		
<i>D. pynaertioides.</i>		

On searching for the structure in specimens from outside the Congo, they are discovered on *D. minutiflora* from all the administrative units of Guinea between Sierra Leone and Nigeria, and on *D. smilacifolia* from Nigeria and Uganda. Moreover, they are discovered on specimens from Sierra Leone which seem to represent the lower parts of the imperfectly known *D. praeheasilis* Benth. (as understood by Vogel's no. 21). The Uganda specimen of *D. smilacifolia* is Dummer's no. 4764.

The Two negroes of the Gold Coast know under the name 'kokora' a forest species which has now been determined as *D. minutiflora*. Kokora, grown by me in the Botanic Gardens, Singapore, for a few years from 1915 produced acarodomatia freely.

This search outside the Congo, therefore, adds *D. prachensis*. All the four species, *D. minutiflora*, *D. smilacifolia*, *D. Pynaertii*, and *D. prachensis* are closely allied members of the section *Enantiophyllum*.

It is useless to seek for ants, acari, or other small animals within the domatia after the plant has been dried, as they desert it when the shelter wilts. Not until observers study these structures in the home of the plants shall we know what uses them.

Dioscoreas commonly have glands which discharge on the lower surface of their leaves, and it seems probable that the pit is a glandular field. That the nerve bounding it should be modified in two ways—by being crested when well developed and by being curved in reverse to the generality of the nerves—indicates that the structure must be regarded as a unit in itself, assertive of its growth against the centrifugal curving of the nerves.

The breadth of the acarodomatia is proportionate to the breadth of the base of the leaf, and the tooth is further away from the petiole the broader the leaf-base, whatever the species. And as *Dioscoreas* produce their broadest and most cordate leaves near the base of the stem, the largest acarodomatia are to be sought near the ground, consequently in the dampest air of the forest—a factor which must help in determining how they are used.

On plants whose larger leaves have them, small upper leaves may be without them altogether.

D. smilacifolia has only its lowermost leaves cordate: the leaves towards the flowering part of the plant are rounded or obtuse below, and in them the teeth of the acarodomatia may sometimes almost touch the petiole as in fig. 2: at other times they are further apart. The genesis of this tooth demands study: the inrolling of a leaf-margin would seem to be something easy in evolution; but the evolution of such an unusual object as a tooth on the lower part of smooth-edged leaves such as the *Dioscoreas* have is strange.

Let it be said, lastly, that the acarodomatia are variable in a considerable degree, though by being so small the variation is not imposing.

2. Twining in both directions in *D. Baya*.

D. Baya is a well-marked species of the section *Enantiophyllum*—a section containing numerous species every one of which without exception twines to the right. But it appears that every now and then something goes wrong with the directional stimulus in *D. Baya*, so that a branchlet twines in the reverse direction. This occasional reversal may be seen in De Wildeman's figure of what he calls var. *Kimpundi*

(Ann. Mus. Congo, Bot. ser. 5, III, pl. 53 ; 1912), but attention was not called to it in the accompanying text. I have verified the plate with the specimen and the twining is certainly to the left. Moreover, Dummer collected in Uganda a specimen of *D. Baya* (no. 859) with a branch twining to the left ; and there is a fragment of stem on a sheet in the British Museum (Natural History) twining likewise.

It would seem as if *D. Baya* is breaking away from the character, deeply ingrained in its section, of twining to the right, as breaking away must have occurred in the past when the sections separated. This breaking away, in the light of our present knowledge, appears as causeless as the change in the direction of the twist of a mollusc's shell.

The PRESIDENT asked whether the domatia described were in reality Acarodomatia and, if so, what was the supposed relation between mite and flowering plant.

He complimented the Botanical Secretary on the first part of the *Dioscorea* monograph written by him in collaboration with Sir David Prain, and expressed the hope that the publication of the second part, now in the press, would not be long delayed.

PROCEEDINGS OF THE GENERAL MEETING

19 January 1939

Mr. J. RAMSBOTTOM, O.B.E., M.A., Dr.Sc., President,
in the Chair

The Proceedings of the General Meeting held on Thursday, 5 January 1939, having been circulated, were taken as read and confirmed.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

Certificates of recommendation of the following candidates for Fellowship were read :—For the second time, in favour of John Frederick Gustav Chapple and Leonard Richmond Wheeler ; for the first time, in favour of Albert Pam.

The President reported the deaths of the following Fellows :—J. O. Borley, O.B.E., Lt.-Col. L. A. Waddell, C.B., C.I.E., W. H. Daun, J. Harris Stone, Montagu A. Phillips, and Commander J. J. Walker.

The President referred to the collective donation of £10 it had been proposed should be made by Fellows of the Society to the Fund being raised to repair the monument to PHILIP MILLER (1691-1771) in Chelsea Old Church yard.

The consideration of a Resolution concerning National Parks was postponed until the next General Meeting.

Prof. R. R. GATES gave an account of Prof. T. S. RAGHAVAN's paper 'Floral anatomy and some structural features of the Capparidaceous flower'.

Abstract.—

Gynandropsis pentaphylla DC. is a common weed in south India. It was found that some flowers in every inflorescence have a small sterile ovary without a gynophore. Over half the ovaries on each plant are sterile. The species is, therefore, andromonoecious. The ovary consists of two carpels with parietal placentae. Each carpel is an inrolled foliar organ, the line of fusion being the placenta. Sometimes an ovary appears to have three or four placentae, but the loculi are then of unequal size. When there are three loculi it is because the fusion is complete on one side but not on the other. Further growth at the point where fusion has failed results in separation of these margins by secondary tissue. When there are 'four carpels', due to failure of fusion on both sides, two of the diagonally opposite loculi are therefore larger than the other two. The gynoecium is thus normally formed by marginal fusion of the carpellary leaves, in accordance with the classical conception of the carpel.

The origin and course of the vascular strands to the various floral organs was traced in *Gynandropsis pentaphylla*, *Euadenia eminens*, *Capparis flexuosa*, *Cadaba indica*, and *Cleome Chelidonii*, with confirmatory evidence that, although the androecium varies widely, the gynoecium is bicarpellary throughout. The inrolling and fusion of the carpel margins is only clear in the very young gynoecium, and the commissure represents, not a solid carpel, but merely the line of fusion of the inrolled margins of adjacent carpels. In most cases each carpel has at first a median vascular bundle representing the midrib and a marginal bundle near each edge. The latter become larger, to supply the ovules, and when the margins fuse the marginal bundles become closely paired and more or less fused later in the commissure.

Capparis flexuosa and *Euadenia eminens* both have extremely small bracteoles which fall off early. The median placing of the outer sepals is also in accordance with the former presence of bracteoles where they are now absent.

Discussion.—

Miss E. R. SAUNDERS said that in the absence of the author she felt some difficulty in offering any comments on Prof. Raghavan's paper. It appeared to her that the account which had been given of the Capparidaceous gynoecium begged the question at issue, viz. the number of carpels present. Stress had been laid on the presence in the ovary-wall of a pair of lateral veins derived from the carpel midribs. This was a usual feature of carpels of the valve type (as of foliage leaves), but it had no bearing in the Capparidaceae on the number of carpels present. For these veins had no connexion with the placentae and ovules, which receive their vascular supply, as in a Crucifer, from bundles situated on the alternate set of radii and serving an alternate set of floral members. The close relation of the Capparidaceae to the Cruciferae required that any interpretation of the gynoecium must hold good for both families and, indeed, for all in which the gynoecium is syncarpous. To describe the ovary of such a type as *Cleome* as bicarpellary did not prove it to be so. The author did not appear to have met in any way the difficulties inherent in the traditional interpretation such *e.g.* as (1) the appearance of the gynoecium in the earliest stage of development (as shown by Eichler and Payer) which could only be interpreted as indicating G2 by ignoring the contradiction between theory and fact; (2) the four sutural contours on the surface of the fully developed ovary; (3) the position of the stigmas; (4) the whole vascular ground-plan; (5) the mode of dehiscence of the fruit, to mention only some of the most obvious ones. These features cease to be difficulties when it is appreciated that the gynoecium is formed of *two* kinds of carpels, sterile and fertile, and that in such a type as *Cleome* $G=4$.

In reply to the remarks of Miss E. R. Saunders supporting her polycarpellary hypothesis, Prof. GATES pointed out that the classical theory gave a more natural interpretation of the vascular anatomy. The figure from Eichler, which she showed, was clearly a later stage of the ovary when the two carpels had already fused. The vascular bundles varied in size according to the physiological needs, and it was impossible to regard the vascular cords as structures having a phylogeny independent of the tissues in which they were embedded.

Dr. J. P. HARDING (Visitor) gave an account of Dr. J. H. DAY's paper, 'A new Cirripede parasite'. [Printed in full below, p. 64.]

Dr. L. RICHMOND WHEELER (Visitor) read his paper 'Deaths among Butterflies'. (Communicated by Dr. W. E. COLLINGE, F.L.S.) [Printed in full below, p. 79.]

**A NEW CIRRIPEDE PARASITE—RHIZOLEPAS
ANNELIDICOLA, NOV. GEN. ET SP.**

By Dr. J. H. DAY, F.L.S., Zoology Department,
University of Cape Town.

RHIZOLEPAS ANNELIDICOLA is an external parasite of the worm *Laetmonice producta* Grube. The host is an errant Polychaet of the family Aphroditidae. Two worms were obtained in a dredging off the Mozambique coast by the South African Fishery Survey Vessel *Pickle*. The larger measured 7 cm. in length and 2.5 cm. in breadth, and had four parasites; the smaller was 2.8 cm. in length and 1.5 cm. in breadth, it had no parasites.

Unfortunately the material was badly preserved. Of the four parasites the first was too badly macerated to be of any use, from the second a series of longitudinal sections was made, from the third a series of transverse sections, and the fourth was dissected out and half of the mantle was removed to examine the appendages. This latter has now been sent to the British Museum as a record. The sections were stained with Delafield's haematoxylin and indicated the broad outlines of internal anatomy, but minute histological details are poor and a fuller investigation of fresh material is required.

I wish to acknowledge my thanks to Dr. C. von Bonde of the Union Fishery Survey, from whom the material was originally obtained, to Dr. W. T. Calman for helpful criticism of this paper, and finally to Mrs. T. A. Stephenson for help in many ways.

External features.—The parasites were attached to the body of the Polychaet between the parapodia. There were three on one side halfway along the body, and another on the other side nearer the tail. In general shape the external portions of the parasites are similar to the parapodia of the host, though a little longer. The largest was 18 mm. long and 2 mm. broad. Dissection proved that this external portion of the parasite is connected with an extensive root-system penetrating the coelom of the worm and matted round the gut. As will be explained later (p. 74) there is some difficulty in dividing the body into cephalic region, thorax, and abdomen, so that the part of the animal which is enclosed within the mantle-folds is here given the non-committal term of 'trunk'. The whole animal may thus be divided into three regions:—The root-system embedded in the tissues of the host, the long stalk, and the trunk enclosed by mantle-folds. (See fig. 1.)

The relation which the structure of *Rhizolepas* bears to that of the familiar *Lepas* is obvious. The root-system is an outgrowth of the stalk which is homologous to the peduncle

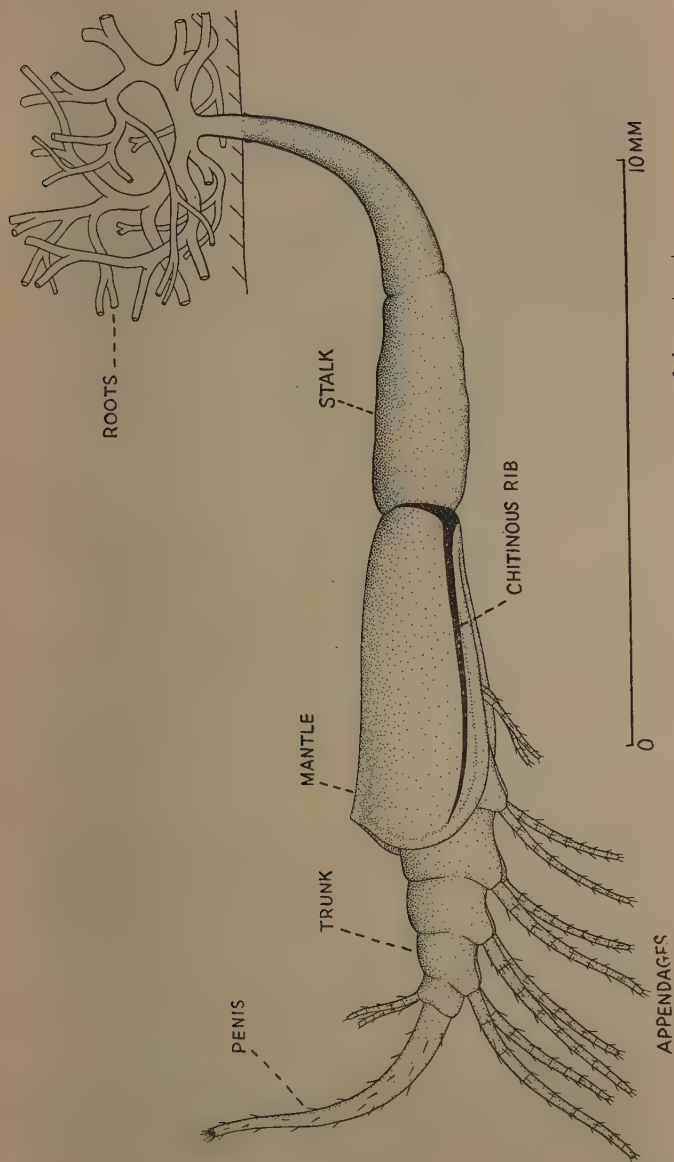


FIG. 1.—Lateral view of *Rhizolepas annelilicola*, showing part of the root-system.

of *Lepas*. The mantle-folds of *Rhizolepas* are proportionately smaller than those of *Lepas* and have no calcareous plates. The trunk is only partly enclosed by the mantle, the trunk-appendages are reduced, and the oral appendages are absent. The symmetry of the two animals is similar, the peduncle being anterior and the penis at the end of the trunk posterior. The mantle is divided into right and left folds, from which the appendages project ventrally.

The trunk is united to the peduncle by a narrow isthmus of tissue from which it soon swells out as a cylindrical body lying freely between the mantle-folds and projecting beyond them to terminate in a long tapering penis. This latter is unsegmented, but is beset with weak hairs along its length with a well-marked brush at its tip. Indistinct constrictions corresponding with the arrangement of the six pairs of appendages divide the posterior part of the trunk, but there is no segmentation anterior to the first pair of appendages.

The appendages are obviously reduced, since they are weak and uniramous. Each arises from a broad base, is jointed, and possesses a number of segmentally arranged hairs. The first pair has about 5 joints, the second 8, the third, fourth, and fifth about 10, while the last has 3. The number of joints given here is only approximate, as the material is poor and the segmentation indistinct. The first five pairs of appendages project ventrally and increase in size posteriorly, but the sixth pair is short and projects dorsally from the root of the penis. The homologies of these appendages will be considered later (p. 75) in relation to the divisions of the 'trunk'. The presence of oral appendages was expected, but careful examination of admittedly poor material failed to reveal any trace of them. They could be found neither in the sections, nor in the examination of a cleared specimen, nor one from which one half of the mantle was removed to uncover the trunk.

Though an alimentary canal is present there is neither mouth nor anus, the only openings on the trunk being those of the reproductive organs. The animal is an hermaphrodite with the oviducts opening on either side of the trunk anterior to the first pair of appendages, while the vasa deferentia unite to form a single tube opening at the end of the penis. Though a pair of maxillary glands were found their openings were not seen.

The mantle arises from the junction of the peduncle and trunk and encloses the latter to which it is united for a short distance ventrally. The two halves of the mantle are joined all along the dorsal surface, but separate posteriorly and ventrally, thus allowing the protrusion of the appendages. Thus there remains an extensive cavity between the mantle

and the trunk which is homologous to the mantle-cavity of *Lepas*, *Anelasma*, and other Cirripedes. The free edges of the mantle are strengthened by thick ribs of chitin which almost meet at the anterior end and then bend round abruptly so as to form a half hoop at the junction of the mantle and the peduncle.

The peduncle or stalk is narrow at the point of attachment to the host, but gradually thickens until it joins the trunk and mantle. It is thus club-shaped, the diameter of the peduncle of the largest specimen being 0.5 mm. at the basal (attached) end and 1.5 mm. at the distal end. The length of the peduncle is 10 mm. and of the trunk 8 mm. The whole body of the parasite is covered with chitin, the covering of the peduncle being particularly thick.

The root-system.—About half the bulk of the parasite is buried within the tissues of the host as an extensive system of branching roots. On dissecting the host it was found that these roots are of various sizes, and branch and ramify in all directions from the peduncle. The main branches are practically the same in diameter as the peduncle and are as heavily chitinized. They spread out just under the integuments of the host and divide into smaller and smaller roots which penetrate into the coelom of the host and cover the wall of the gut.

There is no plan in the arrangement of the roots of the parasite, but the root-tips usually diverge in opposite directions (see fig. 2 A). Occasionally the tips of the roots are expanded and flattened and closely applied to the surface of the gut or to the digestive diverticula of the host, but on no occasion was any root found penetrating any organ. This reminds one of the arrangement of the roots of *Sacculina* and other Rhizocephala, though the roots of *Rhizolepas* are more heavily chitinized than they are in any Rhizocephalan. The root-systems of the three specimens of *Rhizolepas* on the one side of the host were completely interlaced, but it is impossible to say whether there is any actual connexion between the roots of one parasite and those of another. In this connexion it is again worth while referring to the Rhizocephala, in particular to the parasite *Thompsonia* where one root-system gives rise to many externae, and to the work of Perez (1931) on the budding of *Chlorogaster*.

Sections of the roots of *Rhizolepas* (fig. 2 B) show that they are covered with a thin layer of chitin, below which there is a lining epithelium. The interior of the root contains two tubes and irregular connective tissue. The larger tube is irregular and is formed by the coalescence of the spaces between the central connective tissue cells. The smaller tube below it is formed by the invagination of the chitinous

covering. The roots probably absorb nourishment from the gut-wall, the digestive diverticula, and the coelomic fluid of the host. If this is actually the case, the food must be in liquid form as no solid particles were seen either in the lacunar cavities or the chitinous tubes of the roots.

Brief description of internal structure.—The body-wall consists of a layer of chitin, an epidermis, and a weak muscular layer. Inside this are the various organs, and the spaces between them are filled with loose connective tissue.

The distal part of the peduncle contains the ovaries. The oviducts pass into the trunk and terminate in oviducal funnels which open on lateral prominences anterior to the first pair

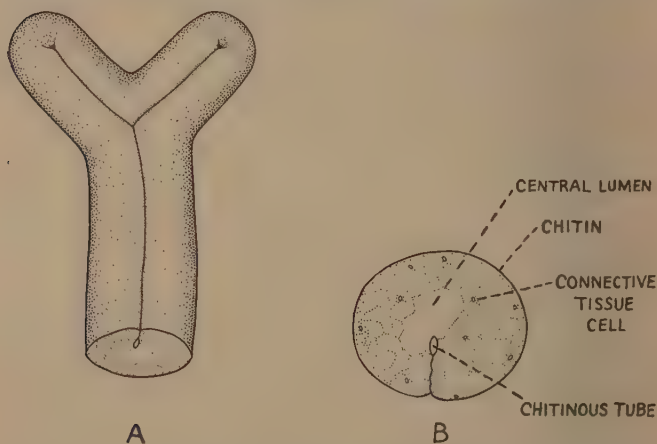


FIG. 2.—A. Portion of a root-tip showing the method of branching and the formation of the chitinous tube. B. Transverse section of a root.

of appendages. The greater part of the trunk is occupied by the testes, from which vasa deferentia pass back and unite at the end of the trunk to form a single ejaculatory duct, which opens at the tip of the penis.

The alimentary canal is merely a tube with an expanded portion or stomach. Both the oesophagus and the rectum are closed.

The nervous system consists of a cord running along the ventral side of the trunk. Anteriorly there is a ganglionic mass giving off nerves to the peduncle.

The body-wall.—The chitinous layer which covers the whole animal varies in thickness. On the smaller roots it is very thin, but gradually becomes thicker on the larger ones until

the maximum thickness is reached at the base of the peduncle. The chitinous investment of the whole peduncle is very thick (0.03 mm.), but becomes reduced where the peduncle joins the trunk. The chitinous covering of the mantle is fairly thick (0.01 mm.) and a special thickening along the mantle-edges forms the strengthening ribs. The chitin on the inside of the mantle and on the trunk is much thinner.

The histology of the root-system has already been described. The epithelial wall of the peduncle is continuous with that of the roots, but differs in detail as a result of the addition of a muscle-layer. The epithelial cells are elongated at right angles to the surface and the nuclei are at the outer ends of the cells. Moreover, the cells are arranged in groups between which the muscle strands are attached to the investing chitin. The arrangement in the trunk and mantle is similar in plan, but the features are not so well marked nor is the muscle-layer always present. Furthermore, parts of the epithelial wall of the mantle seem to contain glandular elements, but the material was not sufficiently well preserved to make this certain.

The muscular layer is complicated. It reaches its fullest development in the peduncle and is there seen to be composed of three layers of muscle-strands. There is an outer and oblique layer of strands which takes a spiral course along and around the peduncle, beneath this is a layer of circular strands, and beneath this again an inner oblique layer encircling the peduncle, but in the reverse spiral to the outer layer. The individual cells composing the strands are all attached to the chitinous walls. The whole musculature forms a basketwork, and probably acts as a single unit allowing the peduncle to be turned and twisted in any direction. In spite of this complexity of structure the whole three sets of muscles take up very little space in the interior of the peduncle, and form no more than a sheath round it enclosing the ovary.

The strongest muscle in the body is a transverse one passing through the anterior ventral surface of the trunk and attached to the chitinous ribs within the mantle-folds. This muscle is homologous to the adductor muscle of other Cirripedes and occupies a similar position just in front of where the mouth should be and where the mantle-folds themselves separate from the trunk. In other Cirripedes the adductor muscle is attached to the scuta and its contraction closes the mantle-cavity. In *Rhizolepas* where calcareous plates are absent it is possible that the chitinous rib represents the remains of the scutum. The ends of the oblique muscles of the peduncle also pass into the mantle and are attached to the edge of the chitinous rib where it bends round dorsally. There are no other muscles in the mantle.

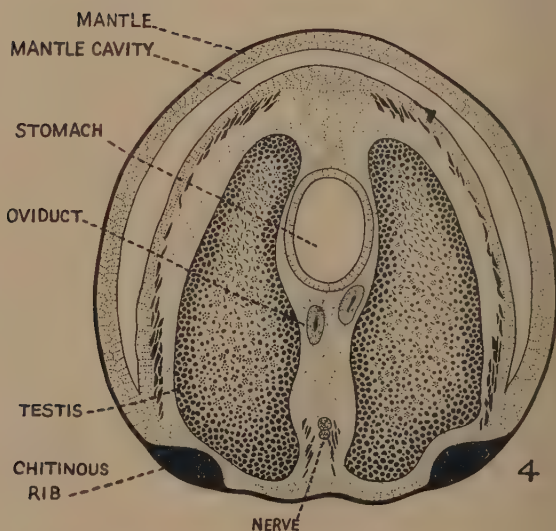
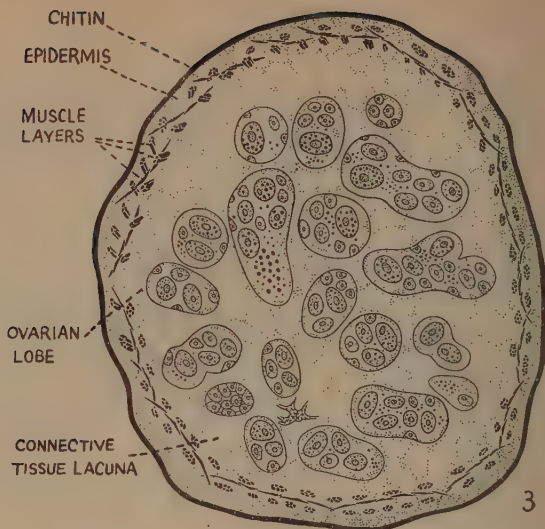


FIG. 3.—Transverse section of the middle of the peduncle.

FIG. 4.—Transverse section of the trunk and mantle near their junction with the stalk.

FIG. 5.—Transverse section of the trunk and mantle halfway between their connection with the stalk and the base of the first pair of appendages.

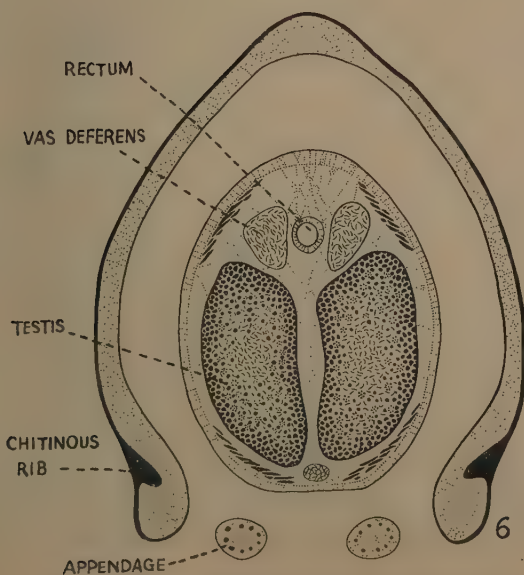
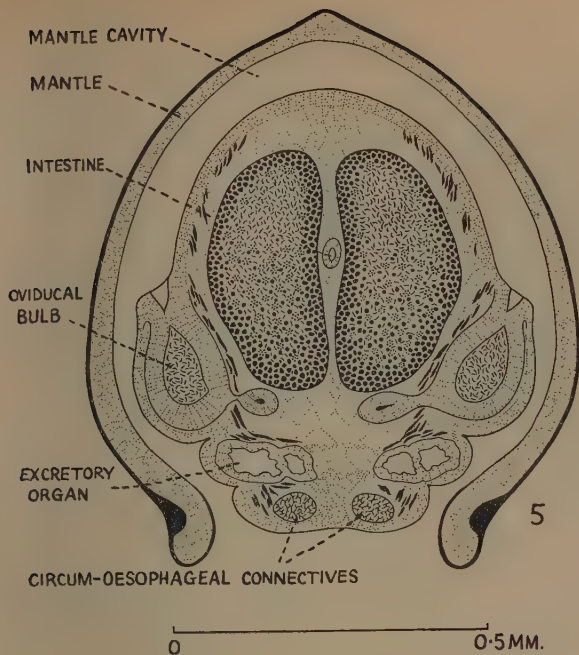


FIG. 6.—Transverse section of the trunk and mantle between the bases of the second and third pairs of appendages.

In the trunk there are three sets of weak muscles. The best marked of these is a layer on the dorsal and lateral sides; a second series is attached to the chitinous wall along the ventral nerve-cord and takes an oblique course to the lateral walls where they are again attached, this series being interrupted by the lobes of the testes. In the posterior part of the trunk a few strands of a third series pass horizontally from side to side between the testicular lobes.

The appendages have weak longitudinal strands along their walls interrupted at the joints.

The reproductive organs.—Female. The ovaries are branching organs situated in the posterior half of the peduncle. All the branches are approximately equal in diameter and are so twisted and closely packed that no plan could be discerned in their arrangement. Since, however, there are separate oviducts it is very probable that there are two ovaries. The ovarian lobes are about 0.1 mm. in diameter; each is lined with an epidermis, but again histological details are uncertain.

From the posterior ends of the ovaries two oviducts may be traced leading into the trunk. These pass backwards on either side of the stomach between the anterior lobes of the testes and finally open into genital atria or oviducal bulbs. The latter are hollow oval structures which lie just inside the trunk-wall, dorsal to the closed oesophagus and anterior to the first pair of appendages. Since in other Cirripedes the oviducts open at the base of the first pair of thoracic appendages, it is possible that this pair is missing in *Rhizolepas*; this question will be discussed later in relation to the division of the 'trunk'. (See p. 75.) In the smaller of the specimens sectioned the oviducts were empty and the lumina of the tubes were not obvious; the walls were composed of a single layer of columnar epithelium, of which some cells appeared to be glandular. In the larger specimen the upper part of the oviduct contained eggs which were similar to those within the tubules of the ovary. Each oviduct opens into the ventral side of the oviducal bulb and the latter opens into the mantle-cavity by a dorsal pore. The walls of the oviducal bulbs were composed of a single layer of glandular cells elongated at right angles to the surface. Johnstone and Frost (1927) consider that the oviducal bulbs of the related genus *Anelasma* act as receptacula seminales. This suggestion now receives support from the fact that the oviducal bulbs of one specimen of *Rhizolepas* contained mature sperm. Apart from their function as receptacula seminales, the glandular nature of their walls recalls homologous structures in *Sacculina*. In his magnificent memoir on *Sacculina*, Delage (1884) showed that there is a structure called the colleteric gland at the end of the oviduct in the form of

numerous sacs whose glandular walls secrete a thin chitinous substance which, when evaginated through the opening of the oviduct, forms chitinous pockets in which the developing embryos are retained until they have reached the nauplius stage. Similar structures in *Lepas* are termed ovigerous lamellæ. It is possible that the oviducal bulbs of *Rhizolepas* form similar ovigerous lamellæ when the eggs are about to be laid, but such structures were not seen in the specimens examined.

Male.—The testes are paired organs occupying the greater part of the trunk. Probably owing to the presence of muscle-strands the testes are thrown into lobes which extend as far forward as the junction of trunk and peduncle and as far back as the base of the penis. Each testis is covered with a thin epithelium below which the germinal cells are budded off into the middle of the organ where various stages of development were seen. What appear to be mature sperm collect in the centre and finally pass into the vesicula seminalis. This is not a specialized organ but merely a cavity in the dorsal side of the testis. This cavity gradually becomes a separate tube which continues back as the vas deferens. The vasa deferentia unite at the end of the trunk to form a single median ejaculatory duct which traverses the length of the penis and opens at its tip.

The alimentary canal.—There is no mouth nor are there any oral appendages. The oesophagus is a narrow tube with a lumen throughout the greater part of its length. The oral end, which is solid, lies just above the ganglionic mass which at this point divides to form 'circum-oesophageal connectives'. The other end opens into a sac-like stomach which represents the crop or gizzard of other Crustacea. This organ lies between the anterior lobes of the testes and has a wall composed of three layers of cells, but there is no indication of a chitinous lining. The stomach is quite empty and there are no digestive diverticula such as are found in *Lepas* or *Anelasma*. From the stomach a very narrow mid-gut leads back between the two testes and joins the hind-gut. This latter has a broader lumen and is probably lined with chitin; it continues back as far as the end of the trunk, but is never connected with the body-wall and ends blindly.

The nervous system.—The nervous system consists of a double cord running along the ventral surface of the trunk just inside the body-wall. In the region of the closed oesophagus, just between the latter and the ventral body-wall, there are two connectives joining the anterior (cerebral) ganglion to a posterior (suboesophageal) ganglion. From the anterior ganglion two large nerves extend forward; one (the left) continues along the ventral surface of the trunk and finally enters the peduncle.

The other bends dorsally, but becomes smaller and is soon lost ; it supplies the region round the stomach. By analogy with other Cirripedes it is suggested that the nerve which supplies the peduncle is homologous with the antennary nerve of other groups of Crustacea.

From the suboesophageal ganglion a double ventral nerve-cord runs back along the trunk. For half the length of the trunk the two parts of the cord are united, but in the posterior part they are separate though very close together.

The connective tissue, lacunar spaces, and chitinous tubes.—It has been noted previously that all the nourishment is obtained from the host via the root-system. This nourishment is distributed throughout the body of the parasite by the connective tissue, the lacunar spaces, and the chitinous tubes.

The chitinous tubes and the lacunae of the roots meet at the base of the peduncle and form a spongy system of tubes and spaces. Thus four irregular chitinous canals were seen at the point where the peduncle is attached to the host ; further up the peduncle the chitinous tubes disappear and the lacunar connective tissue alone is left and this is continuous throughout the length of the peduncle, trunk, and mantle. The cells composing this connective tissue are of the type which have been called ' spider cells ' in *Sacculina* ; that is to say, the body of the cell is small, but there are numerous long processes which connect one cell with the next, so as to leave large irregular spaces between them. These spaces are continuous one with another, allowing fluids to permeate readily to all parts of the body.

Excretory organs.—There are four irregular cavities in the connective tissue of the trunk, two on each side of the blind oesophagus. These cavities represent a pair of maxillary glands which are the excretory organs of the animal, each of which consists of an outer ' labyrinth ' and an inner ' end-sac ' which opens into the former by a minute pore. The end-sacs are connected to one another by a cuticular strip above the oesophagus. No definite communication with the outside was found, but is probably present. The literature on these excretory organs is reviewed by Nilsson-Cantell (1921), who also gives a good description of their structure in the related genus *Anelasma*.

Discussions and conclusions.—Darwin (1851), Gruvel (1905), Calman (1909), Nilsson-Cantell (1921), and Broch (1927) agree in dividing the body of a Pedunculate Cirripede into three regions, viz. : a cephalic region (prosoma of Darwin) which includes the peduncle and the somites bearing the oral appendages, a thoracic region corresponding with the somites bearing the six pairs of cirriform appendages and including

the penis, and a vestigial abdomen represented by the caudal furca. These regions are seldom well marked, and the first segment of the thorax is always fused with the head (Calman, 1909). In a private letter to me Dr. Calman has suggested that the terminal and dorsally directed pair of appendages may represent the caudal furca. This may be so, but their external appearance and internal structure is very similar to the rest of the appendages, which are certainly the uniramous vestiges of the thoracic appendages. Moreover, there are only five pairs of ventrally projecting appendages, so that if the terminal and dorsal pair represent the rami of the caudal furca then one pair of the thoracic appendages must be missing. This possibility is supported by the fact that the oviducts which in other Cirripedes open at the base of the first pair of thoracic appendages, in *Rhizolepas* open on the side of the body just behind the adductor muscle, but well in front of the appendages. Since the mouth and oral appendages are absent the limit of the cephalic region can only be fixed approximately by the position of the maxillary glands and the suboesophageal ganglion. This region also bears the openings of the oviducts, so that there must be a telescoping of somites at the junction of head and thorax.

If the terminal appendages are regarded as a caudal furca then the posterior part of the body is divided into a thorax and a vestigial abdomen. But some doubt remains, and on account of the difficulty of fixing the limits of the accepted regions of the body, all that part which is enclosed by the mantle-folds is here given the non-committal term of 'trunk' and the appendages are called 'trunk appendages'.

Since calcareous plates and oral appendages are absent, the thoracic appendages reduced, and the uncertainty regarding the abdomen there is considerable difficulty in deciding the exact systematic position of *Rhizolepas*. Its parasitic habits, the widely gaping mantle-cavity, the well-developed peduncle, and the arrangement of the appendages mark it off from the Acrothoracica. Again, the absence of sucking mouth-parts, the presence of the peduncle, and the fact that the peduncle does not contain diverticula of the alimentary canal distinguish it from the Ascothoracica. It shows no resemblance to the Apoda, and the presence of an alimentary canal and appendages separate it from the Rhizocephala. The same characters combine to place it in the Thoracica.

Calman (1909), Nilsson-Cantell (1921), and Borradaile in 1931 have given the Cirripedia the rank of a class and the Thoracica is then considered as an order and the Lepadomorpha a sub-order. Geoffrey Smith in 1909 and Broch (1927) give the Cirripedes the rank of order, so that all the subdivisions fall one place lower. While the present writer follows Calman and

Borradaile in ranking the Cirripedia as a class, he has adopted the groupings given by Broch (1927).

Rhizolepas appears to be related to a small group of reduced and parasitic genera including *Anelasma* Darwin, *Koleolepas* Stebbing, *Chaetolepas* Studer, *Gymnolepas* Aurivilius, *Microlepas* Hoek, and possibly *Alepas* Rang. All the later systematists, Gruvel (1905), Pilsbry (1907), Calman (1909), Annandale (1909 and 1914), Nilsson-Cantell (1921), and Broch (1924 and 1927) agree in placing these genera in the order Thoracica and the suborder Lepadomorpha. The division of the Lepadomorpha into families and subfamilies still appears to be a matter of controversy. (See Nilsson-Cantell, 1921, p. 153.) Pilsbry (1907) divided the group into families and subfamilies and united *Alepas* and *Anelasma* in the subfamily Alepadinae: Annandale (1909) made practically the same grouping, but later (1914) united *Alepas* with *Conchoderma* in the family Lepadidae. This is followed by Nilsson-Cantell (1921), but he questions whether it is advisable to tack the other genera mentioned above on to any of the well-marked families. He says, p. 158: 'Wie das Verhältnis zwischen anderen reduzierten Formen wie *Anelasma*, *Microlepas*, *Chaetolepas*, und *Koleolepas* ist, kann man, ohne dass man Material zur Verfügung hat, nicht zu entscheiden versuchen. Auch sind diese Formen so stark reduziert, dass es unmöglich ist, irgendwelche Uebereinstimmungen mit anderen Formen zu finden.' Broch (1927) divides the Lepadomorpha into two large families, the Scalpellidae and the Lepadidae and regards *Anelasma* and *Alepas* as belonging to the latter. He goes on to say, p. 548: 'In dieser Familie bringt man gewöhnlich auch die Gattung *Microlepas* Hoek und *Koleolepas* Stebbing unter; wegen ihrer abweichenden und anscheinend ziemlich reduzierten Organisationsverhältnisse und aus Mangel an eingehenderen Untersuchungen kann man aber ihre verwandtschaftlichen Beziehungen zu den übrigen *Lepadomorpha* zurzeit nicht klarstellen, um so mehr, da wir über ihre Entwicklung nichts wissen.'

As has been shown in the account of the anatomy of *Rhizolepas*, there is considerable similarity between this genus and *Anelasma*. Reference may be made to the lack of calcareous plates, the arrangement of the internal organs, the histological details of the body-wall and musculature, the reproductive and excretory systems, the presence of roots growing out from the peduncle and the absence of what Darwin has termed filamentary appendages.

The differences in structure between the two are mostly related to the methods of nutrition adopted by the animals. The thoracic appendages of *Anelasma* are usually biramous,

though Broch (1924) records a case in which the sixth pair are uniramous. They are always stumpy and hairless and only vague traces of segmentation remain. A caudal furca is absent. Oral appendages, though reduced, are still present, and there is an open mouth, an anus, and a stomach with digestive diverticula arising from its walls. Short roots project from the swollen peduncle embedded in the muscles of the host, which is a shark. Darwin (1851-4), who first described *Anelasma*, considered that it could live and capture prey in the same way as *Lepas*, the roots acting merely as anchors. Johnstone and Frost (1927) were doubtful of this and supported Broch (1919) in the contention that *Anelasma* obtained at least part of its food from the host-shark via the root-system. Since *Rhizolepas* has neither oral appendages nor an open mouth and anus nor digestive diverticula, there can be no doubt that this animal obtains all its food from the host by means of its very extensive root-system.

It may be appropriate here to draw attention to the fact that cement-glands of the type usually seen in the Pedunculata are absent in *Rhizolepas*. An account of their structure in various forms of Cirripedes is given by Broch (1927), who suggests that they are homologous with the antennary glands of other Crustacea. They consist of unicellular glands in the peduncle secreting into minute canals which join to form a main canal opening at the basal (attached) end of the peduncle. The secretory cells lie between the lobules of the ovary, though in *Conchoderma* and *Anelasma* they are present in the mantle as well. Broch says, p. 520: 'Die Sekretkanälchen einiger benachbarter Zellen vereinigen sich, machen in kleinen kugeligen Bildungen von fibrösem Bindegewebe zahlreiche Windungen und erhalten dann eine innere Kutikula.' And further: 'Diese Organisation finden wir in dem Cyprisstadium der operculaten Cirripeden wieder; bei den erwachsenen Formen aber verschwinden hier die Ansammlungen einzelliger Drüsen, und nur der Ausführkanal bleibt bestehen.' It appears, then, that the unicellular glands may disappear, that the ducts may have a cuticular lining and open through numerous pores at the base of the peduncle. Possibly these facts may explain the origin of the cuticular tubes which are found within the roots and the base of the peduncle of *Rhizolepas*.

The structure of *Rhizolepas* throws an interesting light on the relation between the Rhizocephala and other groups of Cirripedes. *Rhizolepas* is not a link between the Thoracica and the Rhizocephala, but it illustrates a grade of organization through which the Rhizocephala may have passed in the course of their evolution. With the loss of the penis and

already reduced appendages and functionless gut, the shortening of the peduncle so that the ovary is enclosed by the mantle, and finally a reduction of the mantle opening, a fair approximation to the structure of *Peltogaster* is obtained; but the Rhizocephala are further characterized by an internal parasitic stage of their life-histories initiated by the Kentrogon stage. The life-history of *Rhizolepas* is at present unknown.

Summary.—*Rhizolepas annelidicola* is a Cirripede parasite of the Polychaet worm *Laetmonice producta* obtained by dredging off the Moçambique coast. It belongs to the order Thoracica, to the suborder Lepadomorpha, and to the family Lepadidae, and is related to the genus *Anelasma*. It is completely parasitic. Uniramous thoracic appendages are present, but oral appendages are absent. There is neither mouth nor anus, but the parasite sucks the juices of its host by means of an extensive root-system arising from the peduncle.

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Dr. W. T. CALMAN called attention to the great interest of *Rhizolepas* as being a type intermediate although not directly transitional between the normal Cirripedia and the Rhizocephala.

DEATHS AMONG BUTTERFLIES.

BY Dr. L. RICHMOND WHEELER.

(Communicated by Dr. W. E. COLLINGE, F.L.S.)

My interest in natural history, particularly in birds, covers some thirty-five years, of which more than twenty-five have been passed overseas, principally in the tropics, in which butterflies most abound in individuals and species. For the last five years, mostly in Malaya, but also in Hong Kong, Canada, Newfoundland, Jersey, and England, I have spent much of my spare time in observing and collecting these insects. I have also given critical attention to the literature of mimicry and other biological theories in connexion with successful work for higher degrees in science at the University of London (External).

In Malaya, where I have lived for seventeen years, in Canada and Jersey at least my own experience in the field and jungle and that of many entomologists and naturalists shows that birds only rarely attack butterflies on the wing, that beak marks are very uncommon, and that injuries to wings indicate that attacks on butterflies are in the great majority of cases made on unconscious butterflies, at rest, and by lizards and many other predators besides birds. This mass of out-door observations, some published and some so far unpublished, is in direct conflict with the opinions expressed by neo-Darwinians such as Sir Edward Poulton, Professor Hale Carpenter, and Dr. R. A. Fisher, which opinions are that the colours of the upper-wing surfaces in butterflies are due to natural selection and that therefore attacks on flying butterflies by the only animals capable of making such attacks to any appreciable extent, that is birds, *must* be sufficiently frequent to provide a *vera causa* for natural selection to act upon colours which in the vast majority of butterflies are only exposed when these insects are flying or alert and ready to fly. And the evidence that birds attack flying butterflies remains but scanty when the abundance and easy visibility of both classes of animals, when flying, are allowed for.

So I have abandoned the neo-Darwinian view of natural selection and mimicry for butterfly upper-wing colours which I used to accept uncritically, like many naturalists. But for a long time I remained puzzled by the excessive attention given to rare cases of bird attacks and beak-marks on butterfly wings by neo-Darwinians, who neglect or misunderstand the

copious evidence which controverts their theories (e.g. Poulton, 1930, p. 519 *a* ; Carpenter & Ford, 1933, p. 68 seq. ; Carpenter, 1936 ; Wheeler, 1935 and 1936)

However, reconsideration of 'Mimicry', published in 1933 by Dr. Hale Carpenter with a collaborator for the genetical section, has indicated the fundamental error on which this abnormal interest in the fate of exceptional butterflies has been based. For it is clearly expressed in the 'formula' which Carpenter suggested as long ago as 1913 and repeated in this book on p. 77. It was designed to show that there must be some check to unlimited increase in butterfly groups supposed by believers in butterfly mimicry to be distasteful to ordinary predators ; and was coupled with the idea that such groups should be unusually subject to attack by parasitic Ichneumon-flies. The formula is as follows :—

'Let X be the total offspring of any pair, then, broadly speaking, $X-2$ is the total number of offspring *destroyed by all enemies* (italics mine—L. R. W.). Putting V for vertebrate enemies, P for predacious arthropods in general, p for parasitic insects, and m for micro-organisms of disease we get the total destruction by enemies as

$$X-2=V+P+p+m$$

and

$$V=(X-2)-(P+p+m).$$

Thus the conclusion is reached that 'If V is very small the other factors must be proportionately greater'.

How true it is that formal logic can be made to prove anything, provided that the premises are suitably arranged. The fallacy underlying this argument is of course that, besides the different classes of organisms mentioned, sheer old age and inorganic physical changes produce death in butterflies, some of them also affecting the earlier stages of egg, larva, and pupa. Among the physical causes are the coming of frost and cold in high altitudes, the fall of tropical rains, the blast of violent storms, and the concomitant destruction of vegetation anywhere, and even a change of wind when butterflies are migrating across seas, as multitudes do every year. And against these accidents the so-called 'models' and 'mimics' are no better equipped than any other butterflies.

Neither I nor anyone else can state what proportion of butterflies meets death from inorganic causes such as these, and it doubtless varies in different places and at different times ; but it is certainly a high one. To take the temperate regions familiar to many entomologists, though certain butterflies are adapted to live through the winter in England and even in colder places such as north Canada, no one who has watched butterflies during a fine warm English autumn and then seen how quickly they disappear when the weather

turns cold or stormy can doubt that such climatic alterations produce a mortality far greater than that due to the birds, lizards, dragonflies, and so forth, which were most numerous and active just when the butterflies were most abundant. And those who have lived many years in the tropics know the diminution wrought among relatively frail organisms by days and nights of continuous downpour or by the sudden squalls, contrasting strangely with the normal hot stillness of the doldrum latitudes, which lay low forest giants, dash leaves and branches together, and sweep them to the sodden ground, the swollen streams, or the floods. It is a difficult matter to prove, but I believe that these tropical storms are largely responsible for the deaths of the butterflies which flit so safely in the warm daylight and are more dangerous than the predators against which they possess powers of concealment and deception, to say nothing of flight. It is certain that during the wet seasons in the monsoon areas of Malaya very few butterflies occur in comparison with the numbers that appear when the weather is mostly fine, and their numbers also dwindle greatly in other districts when intermittent stormy and rainy periods occur; though other factors such as temperature and abundance of food for caterpillars hardly vary at all, while the number of predators certainly does not increase when the butterflies become scarcer.

But though many butterflies, possibly most, meet their deaths through these occurrences in inorganic Nature, not a few die peacefully, from sheer old age, as Dr. Schnack has well described in 'The Life of a Butterfly' (1932). Such is probably the fate of many butterflies observable in the tropics, whose faded colours, frayed and worn wings, and generally shrunk and aged appearance—very noticeable in females which have laid all their eggs—indicate that the vital powers which have lasted for many days, weeks, or months are ebbing away.

So the deaths of butterflies are due sometimes to old age, very frequently to vicissitudes in their physical environment, fairly frequently, probably, to attacks made when they are sleeping or gorging, with wings closed, by a host of predators, among which lizards are the most active in the tropics, and only very occasionally when they are flying or alert for flying, with wings open. These are the facts.

The inductions from them are that:—

(i) The highly varied and usually brilliant upper-wing colours, which are comparatively seldom displayed, have nothing to do with natural selection or mimicry because they cannot affect the usual ways in which butterflies die or run the risk of dying.

(ii) The instances of beak-marks and of bird attacks on

flying butterflies laboriously collected over many years agree with other observations to show that bird attacks on sessile butterflies are moderately numerous and attacks on flying butterflies very uncommon.

(iii) The time and energy given to these exceptional occurrences would be better employed in collecting evidence about all the causes that produce death in butterflies, to which statistical methods might eventually be applied ; or in studying the numerous species about which nothing is yet known except the anatomy and appearance of the imago.

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Discussion.—

Sir EDWARD POULTON said : I agree with Dr. Wheeler that, for the non-mimetic upper surface patterns of butterflies, natural selection does not offer an adequate explanation. When we think of the differences between these patterns in our British *Vanessid* butterflies and their allies in other countries we seem driven to believe in unselected variation, correlated variation, and sexual selection as the probable causes ; when, however, we attempt to explain the origin of mimetic patterns by a cause other than the operation of natural selection I think it must be admitted that no help is to be gained from any hypothesis as yet suggested. The idea, sometimes brought forward, that the resemblance of mimic to model is simply an accidental coincidence was discussed by Dr. F. A. Dixey, who showed that distantly related butterflies bearing similar elaborate patterns, inhabited the same country, but that a simple pattern may appear independently in distantly related species inhabiting widely different countries, but that even these resemblances, which may be fairly claimed as the result of variational coincidence and not of selection—even these are far from numerous. Among the well-known general considerations which confirm the belief in natural selection as the effective cause of the former examples is the fact that the models belong to certain groups of butterflies with warning pattern displayed in flight, but that members of the same group may have entirely different patterns in different countries and are mimicked in each ; also that the mimicking species of a single pattern borne by one or more models in

the same country are not only remote from these in affinity, but also from each other, so remote indeed that day-flying moths are often among them. Concerning the enemies which are believed to have exercised the selective pressure it should be remembered that, although butterfly wings bearing the evidence of attacks which have been actually witnessed are at present few, yet the comparison between these and others entirely confirms the validity of the indirect evidence borne by an immense number of wings collected from many parts of the world for the Hope Department of Entomology in the Oxford University Museum by Professor Hale Carpenter.

Professor G. D. HALE CARPENTER remarked that Dr. Wheeler, like most critics of the current theory of Mimicry, only considered the phenomenon in butterflies. The arguments that he had produced were null and void if mimicry was considered from a wider point of view.

It seemed quite absurd to distinguish between the causes of coloration on under-surface and upper-surface of a butterfly's wing. Dr. Wheeler had admitted that mimicry on the under surface *might* be due to selective attacks of birds upon resting butterflies, but denied the possibility of a similar explanation for mimetic coloration on the upper surface because, he said, birds do not attack butterflies in flight which is the time when upper-surface coloration is visible to them.

But butterflies in nature are not like cabinet specimens mounted to show *either* upper *or* lower surfaces. Very many butterflies when settled on herbage in the sun, or when feeding, open and close their wings, repeatedly showing the upper surfaces, and the argument that a non-flying butterfly only shows its under surface cannot be sustained.

Dr. Wheeler's view would force him to the conclusion, in the case of species with mimetic patterns on the upper surface differing from that on the under, that there must be different explanations for the two sides of the wing. A case of similarity of warning coloration on both surfaces seems equally peculiar on Dr. Wheeler's view. Professor Carpenter dissented very strongly from the statement that birds do not, and indeed cannot, capture butterflies in flight. The study of the triangular marks found on the wings of butterflies, alike on both surfaces, and now known as beak-marks, does not support this statement. Several hundred specimens have been collected together at Oxford from various sources, and the beak-marks are very much more often on one wing than in symmetrical positions on the two wings of opposite sides showing that the butterfly had been seized when at rest with wings apposed. It is realized that a beak-mark on one wing only may have been the result of an attack on a sitting

butterfly, but in that case the coloration of the *upper* surface would have been visible, and this counters Dr. Wheeler's argument that the coloration of the upper surface does not enter into the question because birds do not attack flying butterflies. Moreover, first-hand observations of attack are not so scanty as Dr. Wheeler would have us believe.

Regarding the supposed inability of birds (with some exceptions admitted by Dr. Wheeler) to catch flying butterflies Professor Carpenter referred to Mr. Frohawk's observations of Chaffinches in the New Forest regularly capturing the swiftly-flying Silver-washed Fritillary to give to their young: the Chaffinch is not usually considered to be of very quick flight.

Dr. Wheeler said that the attacks of birds upon butterflies were too few to be able to exercise a selective effect. He might be asked to state what amount of selection he *would* admit as a cause of mimicry, for Professor Carpenter understood that it was the opinion of such an expert as Professor R. A. Fisher that an amount of selection which could not be detected under strict experimental conditions, as being within the limits of experimental error, would be enough to produce detectable changes after a much smaller number of generations than had hitherto been thought necessary. (Cf. Proceedings of the Eighth International Ornithological Congress, Oxford, 1934, published 1938 by the Oxford University Press, page 268 in the speaker's article 'The Attacks of birds upon butterflies'.)

Mr. H. N. RIDLEY stated that he had frequently seen butterflies caught by birds, in England, and that the Falconet, *Microhierax*, in Malaya lived habitually on butterflies and dragonflies and made its nest of their wings, and that in the Pernambuco forests all the specimens of *Morpho* he had caught had the hind wings torn by birds.

Major H. BLACKISTON commented as follows:—That he had been a collector of Lepidoptera for nearly fifty years; it was registered in his memory that he had often seen birds attack Butterflies and had accepted this fact as a natural occurrence.

Of recent years he had been through his private collection and had found a large number of Lepidoptera Rhopalocera showing evidence of beak-marks on the wings. Search was also being made through the large collection of World Lepidoptera, which was being formed at the Booth Museum, Brighton, of which Museum he was Chairman, and a large number of beak-marked specimens were constantly turning up: all such specimens were sent to Professor Hale Carpenter for examination, and, if verified as 'Beak Marks', for his collection at Oxford.

Within the last three years he quoted a case of a Missel

Thrush taking a *Pieris brassicae* on the wing; a female *Euchloe cardamines* being attacked by a Hedge Sparrow; several *Lysandra bellargus* being attacked by Tits; two *Colias croceus* seen flying in from the sea and being found having 'Beak Marks' when captured; three *Vanessa atalanta* being taken within a few yards of the Booth Museum with 'Beak Marks': on one of the latter a piece of wing was missing; the attack was witnessed by a Museum official and the victim thus captured. All the above-mentioned specimens have been accepted by Professor Hale Carpenter as 'Beak Marks' and have been presented to him.

Lastly, he had drawn the Professor's attention to a report which appeared a few days back in the 'Sussex Daily News' from an eye-witness of an attack by a bird on a *V. atalanta* in one of the busiest streets of Brighton's centre—namely, Preston Street.

Through the courtesy of the Editor of that paper he had been able to put the Professor in touch with the eye-witness (a Mr. Fell) of the attack, with satisfactory results as to details.

There was not the least doubt that large numbers of Lepidoptera Rhopalocera are attacked by birds; most of his many Entomologist friends have mental registrations of having witnessed such attacks; and the number of attacks seen is probably small in relation to the number of attacks which occur.

Whether birds attack from a hunger urge or in the spirit in which a dog will run a moving cat it is impossible to say—probably these motives both play their part in arousing such volition.

He could not speak about attacks in the tropics to any extent, as his attention there was devoted to collecting Anopheline Mosquitos and Tabanidæ flies for the late Sir Patrick Manson.

Mr. N. B. KINNEAR said that in 12 years' experience in India he never saw a bird attack a butterfly.

Captain C. DIVER pointed out that the omission of the cataclysmic and old-age death-rates would not, as Dr. Wheeler seemed to assert, invalidate Professor Carpenter's argument. The population to be considered was that of the actively breeding adults. And if before or during the breeding period a steady selective attack, even though small, were made on the imago, it would result in preventing certain forms from contributing their full quota to the next generation—a process which in the course of time should produce the results claimed.

Dr. HUGH SCOTT regretted that Brigadier W. H. Evans could not be present, as he would have contributed to the support of some of the main points in Dr. Wheeler's thesis.

Dr. Scott himself could only speak from a neutral standpoint. On his expeditions in various parts of the tropics, spread over thirty years and varying in duration from a few weeks to eight months at a time, he could not recall ever seeing a bird chase a butterfly; he did not therefore deny that such incidents occur, but he would have noted them had he witnessed them. In England he had occasionally, at long intervals, since he was a boy, seen birds chase (not necessarily catch) butterflies and day-flying moths. The cases most vividly remembered concerned the House-sparrow, the Common Fly-catcher, and a species of warbler, either the Willow-wren or the Chiffchaff.

It may be recalled that the late Col. C. G. Nurse, who had over twenty years' experience in the East, published in 1903 a paper entitled 'The enemies of butterflies' ('Journal of the Bombay Natural History Society', xv, p. 349), in which he supported a view then recently expressed by the late Col. Yerbury*, namely, that attacks by birds on butterflies are comparatively rare, but occur more often in damp than dry districts. This was referred to by Dr. Scott in his obituary notice of Col. Nurse ('Entomologist's Monthly Magazine', lxx, p. 21; 1934).

Mr. H. W. PUGSLEY suggested that the marks on butterflies' wings might be sometimes due to the insects' pugnacity. He had watched a male Silver-washed Fritillary repeatedly attacking a large Dragon-fly.

In replying, Dr. WHEELER said: I understood Sir Edward Poulton to agree that most attacks by birds are made on butterflies at rest, as indeed he indicated in his article on 'Mimicry' in the 'Encyclopaedia Britannica', 1930 (xv, 519 a); and that there is 'an immense lot' of 'natural deaths'. I therefore deprecate the frequent use of pictures of upper surfaces of butterflies in works on mimicry, as in that article and Fisher's 'Genetical Theory of Natural Selection' (pp. 156-7). Butterflies normally rest unconscious with wings closed and upper colours hidden.

I much appreciate Professor Hale Carpenter's kind personal reference at my first appearance before the Linnean Society; our controversy concerning butterflies has increased my circle of friends. He says correctly that I admit the *possibility* of mimicry on under-wing surfaces, as I did in 1935 ('Science Progress', p. 118, p. 275). To his statement, with which I agree, that semblance of mimicry is commoner on upper than under surfaces I reply that the admittedly smaller amount of apparent mimicry on under surfaces indicates

* In 'The Bionomics of South African Insects', Trans. Ent. Soc. London, 1902, part iii. Col. Yerbury's views were summed up on pp. 360-1.

that mimicry in butterflies cannot be very important, because butterflies at rest are exposed to attacks from many predators, while flying butterflies are largely exempt from attack.

My opinion that it is very difficult for insectivorous birds to capture healthy butterflies in flight is shared by Marshall (Trans. Ent. Soc. 1909, p. 138) and supported by Dr. Hale Carpenter himself in 'Mimicry' (p. 68) and by Swynnerton's 'Investigations into the Defences of Charaxes Butterflies' (pp. 483, 488).

Dr. Carpenter and another speaker claimed that Carpenter's formula is still partly or wholly valid. I cannot admit this, because it takes no account of the large mortality among butterflies due to physical causes or of those that live till they die from old age. One speaker claimed that the only significant mortality is that among freshly emerged butterflies. This, I consider, is incorrect; many females lay eggs singly, take much trouble about their deposition, and need many days for the business, at least in Malaya. They are unlike the silkworm moths of our childhood. Incidentally, young butterflies are the swiftest and hardest to catch on the wing.

In Malaya, at least, paired injuries are much commoner than those on one side only; and seem due mostly to lizards and other non-avian enemies.

Mr. Ridley mentioned the Malayan Falconet. It is not a particularly common bird (cf. 'Birds of Singapore Island', p. 104). It does occasionally capture flying butterflies and is said to line its nest with lepidopterous wings; but I have not heard how these are known to be from butterflies and not from moths.

As regards frequent assaults by birds on butterflies in Matto Grosso, Brazil, Schaus and Punnet considered that records of such attacks in South America are very rare ('Mimicry in Butterflies', p. 112). The absence of definite reports by Bates, Belt, Wallace, and other pioneers of the butterfly mimicry theory is astonishing to those who have read their works (cf. Marshall, *op. cit.* p. 383). (Collenette's beak-mark percentage for Matto Grosso is only 1.9.)

During ordinary rain-showers or storms butterflies do shelter under leaves etc., as Mr. Ridley said, and emerge when the sun shines again. But this does not apply to prolonged torrential rain and violent storms which occur in Malaya and other tropical places or, perhaps, during an English July.

No speaker attempted to controvert my argument that in autumn butterflies continue numerous in fine warm weather while their supposed persecutors are also numerous, but vanish when cold or continuously stormy weather comes; though very few species hibernate in the imago state.

My argument is not disturbed by occasional attacks made

on flying butterflies by birds, such as the five mentioned by Major Blakiston, nor by the finding of occasional beak-marks, mostly on one side according to Professor Carpenter, 'frequently' on both sides according to Collenette. Of occasional assaults on flying butterflies a relatively high proportion involve the Common Sparrow and Common White Butterfly, both in England (e.g. Collenette, Proc. Zool. Soc., 4 July, 1935) and North America, in which areas these creatures are parasitic on Man and his vegetables and therefore occur in unnatural quantities. This agrees with Mr. Hugh Scott's seeing Sparrow attacks in England, but none in the tropics.

I welcome also the statement of Mr. Kinnear, an ornithologist with twelve years' experience in India, who never saw any bird attack a butterfly. These two agree with the much longer experience of Mr. T. R. Hubback, Game Warden in Malaya, and Mr. Piers, Curator of the Nova Scotia Museum, and other naturalists, and indicate that attacks on such obvious creatures as flying butterflies are quite rare.

I appreciate that Dr. Carpenter only counts what appear to be genuine beak-marks, and I admit that such things exist. But Mr. Kinnear's doubts about some beak-marks should be borne in mind.

I regret that Brigadier Evans and Dr. Walter Collinge were unable to attend this meeting; and that lack of time prevented me from quoting numerous observers in Malaya, Canada, and Jersey.

PROCEEDINGS OF THE GENERAL MEETING

2 February 1939

Mr. J. RAMSBOTTOM, O.B.E., M.A., Dr.Sc., President,
in the Chair

The Proceedings of the General Meeting held on Thursday, 19 January 1939, having been circulated, were taken as read and confirmed.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

The following Fellow signed the Obligation in the Book of the Charter and Bye-Laws and was admitted :—Robert Roderick Broome.

Certificates of recommendation of the following candidates for Fellowship were read :—For the second time, in favour of Albert Pam; for the first time, in favour of Debabrata Chatterjee, Balai Chand Kundu, Walter Samuel Millard, and Joseph Burt Hutchinson.

The consideration of a Resolution concerning National Parks was postponed until the next General Meeting, after the PRESIDENT had read an amended Resolution submitted by Dr. JULIAN HUXLEY.

A Discussion on 'Subspecies' and 'Varieties' was held, in which the following spoke :—Mr. M. A. C. HINTON, Dr. W. B. TURRILL, Mr. A. J. WILMOTT, Mr. J. S. L. GILMOUR, Mr. H. W. PARKER, Dr. B. P. UVAROV, Prof. C. E. McCLUNG (Visitor), the PRESIDENT, Mr. C. E. HUBBARD, Prof. F. E. WEISS, Dr. J. HUXLEY, Dr. R. MELVILLE, and Prof. W. GARSTANG.

A DISCUSSION ON 'SUBSPECIES' AND 'VARIETIES', arranged at the request of the Association for the Study of Systematics.

Mr. M. A. C. HINTON, Sec.L.S., said in opening that the discussion had been arranged in response to a request from the ecologists and geneticists of the Association for the Study of Systematics for information as to the views and principles (if any) governing the practice of systematists in dealing with 'subspecies' and 'varieties' in various groups of animals and plants.

Mammalogists had not troubled much about 'varieties' from a systematic point of view during the last 50 years. On the other hand, 'subspecies' were defined and used to express stages or trends in geographical variation, i.e. they corresponded to points on Huxley's 'clines'; the characters used for establishing these subspecies were mostly rather small external differences of colour and size, which might, of course, be correlated with differences of size or proportion in the skulls and teeth. To some extent these characters were *adaptive*; they might follow regional changes in climate or other environmental circumstances or they might be purely local.

The principle worked to by most mammalogists was that no two subspecies could ever be found on the same ground. Though generally right, this was not right in all cases, e.g. in certain rats and squirrels where a long course of migration and variation had been pursued and where it sometimes happened that two subspecies of the same species after very different histories and journeys met once more on the same

ground. These could exist side by side for some considerable time provided that they occupied slightly different stations on the same ground.

Another principle adopted by many was that you could not determine a form as a subspecies of a species unless you could demonstrate intergradation—it was said that you bit off too much theory if you acted otherwise; so, failing intergradation, you made a new species—often on the most trivial grounds. It was possible to push all views and theories too far. This one broke down very conspicuously in the East Indies, e.g. in the Mergui Archipelago, where one had perhaps 7,000 islands each with a Fruit Bat, Tree Shrew, Shrew, Squirrel, and Rat, each just distinguishable if you had enough material, from its representatives on neighbouring islands and the mainland. Intervening water prevented intergradation, and all these forms, if this principle were upheld, would have to be treated as 'species'—which was ridiculous.

Another consequence was that the thread connecting all the related forms was broken into short lengths; no mammal had a range; and that most interesting and instructive phenomenon, discontinuous distribution, disappeared beneath a load of unnecessary specific names.

The definition of subspecies was an essential step in any intense analysis of the facts of variation and distribution. In dealing with the fossil mammals of the later geological horizons it also was of tremendous importance—preventing people from making loose identifications of mammalian remains and the false geological reasoning often based upon bad identifications.

It is hoped, shortly, to inaugurate a great series of large-scale experiments on Mammals, Birds, and other animals—partly on the lines of Sumner's classic experiments on *Peromyscus*—to test the values and permanence of subspecific characters in various groups. In the course of the next few years we hope to get definite information on all sorts of points connected with this subject on which at present surmise alone is possible.

Dr. W. B. TURRILL, F.L.S.:—This discussion on Intra-specific Units must be regarded as exploratory—otherwise, it is premature. The Association for the Study of Systematics has found that there are so many subjects, in or related to taxonomy and fundamental to it, that are in need of the most careful and thorough re-investigation that it will require many years of loyal and hard work on the part of its members before sound and generally acceptable

conclusions can be reached. The fact that numerous uncertainties, ambiguities, instances of lack of precision, and basic disagreements are being discovered in its very valuable discussions, so far justifies its existence. The Association has not yet had time to solve more than an insignificant number of these difficulties, and before this can be done it is essential to obtain the greatest possible amount of help from all biologists. Taxonomy is the basis of biology, and it has, therefore, to be conservative, since changes in its concepts, methods, terminology, or nomenclature upset others than taxonomists. This discussion gives us the opportunity of putting forward a variety of personal opinions and experiences, and at the same time of asking for the active interest and help of our colleagues.

Taxonomy is the oldest branch of biology. There is a long history behind botanical classification, and this historical development is important because we are still, partly consciously but largely unconsciously, partly with advantage but partly with disadvantage, bound by tradition and custom. For example, the first part of Art. 10 of the International Rules of Botanical Nomenclature, 1885, reads: 'Every individual plant, interspecific hybrids and chimaeras excepted, belongs to a species (*species*). . . .'. In this article and in the rules as a whole there is no separate accommodation for apomicts or for 'species in the making'. These must, therefore, either be left without taxonomic status, be included under species, or raised to the rank of species—to the further confusion of the species concept in theory and practice. One suspects that the Rules are still largely limited by pre-evolutionary views. The difficulty of dealing nomenclaturally with a dynamic situation is, one acknowledges, very great, and botanists have every reason to thank those who have done their best to make a working set of rules.

The thesis I wish to put forward for discussion is that all taxonomic categories are matters of scientific convenience based on abstractions from what is at the taxonomic level essentially a continuous evolution which is still an active process. One would on this view expect to find every possible grade of distinctness between accepted species and intra-specific units, and every possible degree of polymorphism within species. This evening we are concerned especially with intraspecific variation, and the attempts to classify what Mr. Norman of the British Museum has suggested to the Association might be termed paramorphs. It is, I think, impossible adequately to consider intraspecific variation without bringing the species concept itself into discussion, but I will avoid doing that as much as possible.

Very broadly, one can distinguish between an alpha taxonomy (approximately equivalent to the ecologist's primary survey) and an advance from this towards a perfected or omega taxonomy which is an ideal. In areas whose flora is only now becoming known it is generally desirable not to analyze below the species level and even species must often be accepted as very tentative. In a flora as well known as that of the British Isles much more material and many more data are available, and the problem begins to take on a different aspect. I say 'begins' because our ignorance regarding common British species is still very great indeed except from the gross morphological and phytogeographical standpoints. One can, however, as a starting-point for intraspecific research, most often accept the species as they are defined in, say, the last edition of Babington's Manual. My plea is that such species should be intensively investigated one by one or, better still, in small groups, by as many methods as possible—concentrating on the group and not on the method. Taxonomic advance at and below the species level can only be brought to full possible success by increasing the number of criteria used. This involves controlled experiment and extensive field investigation as well as laboratory, herbarium, and library studies. These combined methods have, in the several groups in whose investigation I have participated, shown invariably that the problems of intraspecific and interspecific taxonomy are much more involved than is generally stated. Species are much more polymorphic than published descriptions usually suggest. Their plasticity can never be correctly estimated except after extensive experiments. There are all sorts of unexpected overlappings between characters due to reaction of one genotype to different environments and those due to different genotypes in the same or different environments. It is often impossible to define, except arbitrarily, a unit character. Hybridization between species and between intraspecific units is of all grades of intensity and frequently upsets nicely postulated schemes. Isolation is due to a variety of causes and is of every possible degree. Time will not allow of detailed examples and I can only refer to the published work of Marsden-Jones and Turrill on *Silene* (series of over 20 papers in the 'Kew Bulletin' from 1928 and still in process of publication), on *Anthyllis*, *Saxifraga*, *Centaurea*, and *Ranunculus* in the 'Journal of Genetics', and on transplant experiments in the 'Journal of Ecology'. We have a large number of experiments still in progress, and it would be unwise to anticipate our final conclusions beyond suggesting that they may not find immediate favour among orthodox taxonomists.

Before proceeding, may I reiterate that the work of the alpha taxonomist is not only valuable but indispensable and must be taken as the starting-point for all future research? If in the course of such research a new taxonomic outlook is reached this is not necessarily derogatory to the pioneer work.

Intensive studies, particularly in *Silene* but also in other genera such as *Centaurea*, and less intensive studies such as those on *Ajuga* and *Fraxinus* (published in the 'New Phytologist') and on *Glaucium* and *Clypeola* (published in the 'Kew Bulletin') lead without doubt to the conclusion that taxonomic categories in some genera at least intergrade completely and that intergradation is also frequent between the constituents of any one category. This does not mean that examples cannot be quoted of genera etc. which are monotypic and whose isolation is marked (e.g. *Adoxa*, *Welwitschia*, *Ginkgo*). A protest must, however, be made against selecting a few examples to establish a positive generalization. This is false logic, but is a device often resorted to. Even with such examples, a fundamental abstraction is ignored: that the category (species etc.) is restricted to what is existing at present. For example, the work of palaeobotanists, as recently summarized by Sir Albert Seward, shows clearly that it is impossible to regard *Ginkgo biloba* as a clear-cut species or the genus *Ginkgo* as a clear-cut genus, except by abstraction of the existing individuals from the sum-total of known specimens including the known fossils. For most other monotypic genera and isolated species or intraspecific units the distinctness of a group is again demonstrable for the existing flora, but the group is isolated on the time-scale only by our ignorance of its phylogeny. Even within the existing flora of the world taxonomists unavoidably use abstracted material and data to an extent that is often forgotten. Samples in all the herbaria of the world together are rarely adequate, for the vast majority of species they are extremely meagre, and additional material frequently involves a change in conclusions.

All this sounds depressing and I may again be accused of defeatism. I am, however, convinced that attempts to build on false assumptions and to slur over difficulties is the way to ultimate defeat, while a frank acknowledgment that our concepts and methods are means to an end, continually needing overhaul, and justifiable only so far as they solve problems and open up new fields for research, can lead us nearer the goal of a perfect taxonomy. I am indeed optimistic that the newer methods, especially of experimental taxonomy, will throw a flood of light on the difficulties of intraspecific variation—as, indeed, they are already doing.

The number of terms used by one or more biologists to designate intraspecific groups is very large. Mr. A. J. Wilmott is collecting such terms for the Association, and I would support his anticipated appeal for assistance. In the taxonomic field the most widely used intraspecific categories are subspecies and variety. One cannot study these adequately except on the basis of characters. Firstly, one has to distinguish fluctuations from characters due to genotypic differences, and this is not always an easy matter, except by experiment. Assuming, that this is done the genotypic characters, morphological and physiological, have to be determined for individuals of as many samples as possible and their plasticity estimated and allowed for. Then the degree of coherence of characters has to be determined and correlated with the factors of isolation (ecological, cytogenetic, phytogeographical). To every phenotype which is the expression of a different genotype the term variety may be given. Since genes and their allelomorphs are for some species very numerous, the number of theoretically possible varieties for some species runs into millions. Occasionally certain genes or gene combinations have a limited distribution within the species population. Such limitation may be due to youth of the mutation, or to the selective action of climatic, soil, or biotic factors. There are, however, many characters which, so far as we can judge, have no selective value (for example, anthocyanin or its absence in immature seeds and armadillo and tubercled testas in *Silene*)—and the distribution of these sets some problems at present unsolved. Occasionally a portion of a species is partially or completely cut off from breeding with the remainder. This isolation may be ecological leading to the formation of ecotypes and ecological species (as *Silene maritima*), cytogenetical leading to the formation of distinct convivia, commiscua, and comparia, or phytogeographical leading to the formation of geographical subspecies. There is no exact point where such isolation steps from varieties to ecotypes, commiscua, etc., and subspecies, and these to species. It is so much a matter of scientific convenience (not, be it noted, mere convenience or mere taxonomic convenience) that I am prepared to admit that for one purpose a group may best be considered a variety, for another a subspecies, and for another a distinct species, though this may not often happen. On the whole, the botanist considers as distinct species what many zoologists would, in animals, term subspecies. This is, I think, justifiable, because cytogenetical barriers to crossing are relatively less important and ecological barriers probably of relatively greater importance in plants than in animals. There are, for example, no

psychological mating or home-choosing preferences in plants, and the higher plants and the majority of the lower ones are not self-motile, though they may be more easily moved by natural dispersal agents than many animals, as seeds or spores, including pollen. Personally, I think the term subspecies should be used as little as possible and only when the evidence is reasonably clear that a species is in process of breaking up into or is throwing off new ones. This only gets over a part of the difficulty of giving 'species in the making' a taxonomic status, because species can be formed in other ways, e.g. by hybridization. The possibility and desirability of different schemes for different major groups of animals and plants and also the possibility of a sort of sliding scale which might extend the conception of 'clines' put forward by Dr. Huxley need full investigation and wide consideration.

Apomicts I consider quite definitely, as I explained to the Society last Session, need distinct taxonomic treatment. They are neither varieties nor species. The question of names for intraspecific units I should again consider on a purely pragmatic basis. They should only be given when they fulfil a need beyond that of drawing attention to their author. Sometimes they are needed, as in some ecological, cytogenetical, or other research, or for horticultural or other economic purposes. Most often names are not essential for progress in the study of intraspecific units and may indeed obscure essential facts. To name the uncounted thousands of character combinations occurring in *Silene Cucubalus* and *S. maritima* would be absurd. Yet they have to be studied if one is to understand the species themselves. Marsden-Jones and Turrill have, therefore, been experimenting with a scheme in which letter and figure symbols are used to represent characters. Such a scheme has proved its value for genetical and population studies in *Silene* and for variation and phytogeographical studies in *Glaucium*. It is not perfect, but has the great advantages of being elastic and comparative.

In conclusion, my present personal standpoint is this: we need, firstly, a complete and critical survey of existing taxonomic concepts and methods, and, secondly, an encouragement of research on interspecific and intraspecific problems, on as many species as we can find workers to investigate, but by synthetic methods. Till the Association provides what may be the equivalent of a Royal Commission Report, and until many more species have been investigated along the general lines used for the studies on *Silene*, I think we shall do well not to make laws of the Medes and Persians for the use of such terms as subspecies and variety.

A. J. WILMOTT, F.L.S.:—Subspecies and varieties are merely two of the terms used to denote categories of variation observed in Nature. The same terms are used to denote groups of different rank in the nomenclatural system. The use of the same terms for both philosophic and nomenclatural purposes is the chief cause of the confusion which regularly appears as soon as discussion of these matters arises. Different systematists choose different categories of variation to which to apply the biverbal names which nomenclators agree shall be given to what they call species, i.e. taxonomic species, a taxonomic species being defined as a biverbal name the connotation of which is specified by a specific definition.

Now the word species is merely a classical synonym of the word kind; by species we should mean the different *kinds of organisms* into which we can group all the individuals constituting Organic Life. Naturalists *believe* in the existence of natural species; they observe that individuals *can* be united into groups characterized by the possession of distinctive heritable correlated features (distributed throughout the organism), and that such groups always possess distinct distributions (due to the history peculiar to each group). The differences between these groups may be many or few, obvious or obscure, but each group keeps its specific differences and reproduces its own kind and no other. Species, like genera and families, may be big or small, but in spite of this the idea still exists that the biverbal names should indicate groups of comparable *size*. An attempt is therefore made to give the obvious and distinct kinds biverbal names, and to unite into 'collective species' systems of closely related smaller species, each of these smaller species then being called a subspecies (or until comparatively recently in botany, a variety).

To my mind such a procedure confuses matters. It would be better to eliminate the word species from nomenclature and replace it by such a term as 'binome', i.e. a group to which a biverbal name is applied. The term subspecies in its nomenclatural sense would similarly be replaced by that of 'trinome'. Such procedure would leave naturalists free to discuss without verbal confusion the different kinds of species in Nature, and how many different categories of variation they could distinguish. The nomenclators would be left equally free to debate which of these categories or groups it was desirable to treat as binomes or trinomes.

To my mind the true subspecies are merely parts of the present time section of a lineage which has become branched by isolation, when the branches have not yet become completely separated by the development of any *absolute* criteria. Although the small species of the *Onosma echioides* group

are mostly completely identifiable and occupy distinctive areas, only of a certain percentage of individuals could I say, by mere inspection, whether they belong to the Neapolitan or Illyrian stock. Possibly further study would show that other and absolute distinctions exist and that these two lineage branches are as distinct as the rest, but at present they are to me an example of true subspecies, i.e. groups of which the criteria are *specific in type*, i.e. correlated genetic differences coupled with a distinct distribution, but they are not absolute differences, i.e. phenotypic intergrading occurs. I say *phenotypic* intergrading occurs, because I should expect to find that individuals of each subspecies would, if cultivated, be found to have and to keep the variation curve of its subspecies with its own definite norm and coefficients of correlation.

Thus we already can distinguish the categories of *simple species*—undoubted species—which are easily recognized and are not closely related to any others, *collective species*, which consist of a group of *small* (but distinct) *species* similar in kind to 'undoubted' species but with smaller differences and as a rule with lesser areas of distribution because they are more recent fragmentations of previously wide-spread species. When intergrading occurs and no absolute differentiae can be found, we have *subspecies*, sometimes quite small subspecies. Such *small species* or *subspecies* may be very small when each small island or rock bears its own slightly distinct form of a species, or within a wide-spread species, relicts occupying isolated habitats have in surviving undergone differential selection (such as the ecotypes of Turesson). In snails, I am told, similar phenomena occur in groups which are merely local populations, which in one informal discussion were dubbed 'micropops'. But all these categories, except perhaps the last, appear to be of the 'species-type' of variation, similar in kind though different in degree. To which or how many of these categories the term subspecies should be applied may be arguable, for there certainly is yet no agreement, but the matter should be settled without very great difficulty, although there may be species of different origins and other pseudospecific categories. There is, however, another series of categories of variation in which we are not dealing with different kinds of organisms, but only with the observed phenotypic effects of separate genes, which in a previous discussion in this room (4 April 1935) I alluded to as 'phenes'. Thus we find white varieties of different species of *Viola*, broad and narrow-leaved varieties of most of the species of *Salix*, and so on. Moss, in 1912, wrote a paper drawing attention to three pairs of phenes in *Stellaria Dilleniana*, three combinations of which had received biverbal

names as distinct species, and some but not all of the others varietal names. It is possible that such similar variations in allied species may be due to the *same* genes existing in the different stocks. Simple mutations are often of this nature, and in variable species a large number of these phenes, or their various combinations, may be given distinctive names, as varieties, aberrations, *lusus*, and so on. My view is that these should not be given names under the same system of nomenclature as the species and subspecies, for we are not here dealing with different kinds of organisms which always reproduce their kind, but only with different genes, which are analogous, in a sense, to the mere bricks of which the house is built. Such variations must be studied, but such studies should be recognized as investigations of genes (phenes) and their distributions, quite distinct from studies of kinds of organisms and *their* distributions. A separate kind of nomenclature and method is required for each study. Possibly the local snail populations should be investigated thus, for they may be merely products of the accidental gene constitution of their founders. We need to know the frequency and proportions of these genes throughout the area of the species concerned. Weismann termed his heritable units 'ids' and we might name phenes in some new way, e.g. 'albido' and 'colorido', 'angustifolido', and 'latifolido', and under these names give the proportions of each in any area. It would, however, be simpler to use a system of letters—used uniformly within any critical group—such as is done in genetics, possibly using the Latin alphabet to indicate genes and the Greek to indicate phenes not yet genetically analyzed.

If the term 'variety' is used at all, I should prefer to retain it as signifying a variation the nature of which is not yet known, i.e. as corresponding simply with the idea of 'variation'. In relatively unworked areas it is often impossible to say whether a given variation, as exhibited by a specimen, is of specific type or merely an unusual (or merely not previously observed) accidental conjunction of separate phenes. Some systematists object to this view, and say that the term variety has now a definite special taxonomic significance. To this I cannot assent, for to those whose binomes are the collective species, the subspecies of other workers become varieties. In fact, I think it fair to say that *none* of these terms has at the moment any definite meaning at all because each has so many different meanings.

Let us therefore first set out to discover how many categories of variation we can distinguish in Nature. Let us define these and if necessary give them distinctive terms. Then let us consider quite separately what is the best way to

classify and name them and decide which category or categories shall be regarded taxonomically as binomes, which as trinomes. Then we may begin to see the end of these discussions concerning what is a species, what a subspecies, what a variety, for each of these will be a term denoting a known and recognized category of variation instead of being a more or less meaningless source of dispute.

It should not be very difficult to do this, for the categories are mostly, I believe, fairly well known. It is only because of the intrusion into the taxonomic problem of the exigencies of nomenclature that no agreement has yet been reached as to what each category should be termed.

Mr. J. S. L. GILMOUR, F.L.S., dealt with the philosophical aspect of the subject and defined taxonomy as that classification of living things which is based, as far as possible, on total attributes, and which can, therefore, be used in making a wide range of inductive generalizations. In addition, there are many 'non-taxonomic' classifications, based on a selection of attributes and useful for special purposes. Both types of classification are necessary for a proper treatment of infra-specific variation. Taxonomic categories, based on total attributes, might be confined to subspecies, variety, and form, while a series of 'non-taxonomic' categories, based on such selected attributes as intersterility and interfertility, geographical distribution, etc., would be necessary. Examples of the latter are Danser's commiscuum, comparium, and convivium, and Vavilov's 'geographical groups' in many cultivated crops.

Mr. H. W. PARKER, F.L.S.:—Systematic Procedure in Herpetology' has been ably outlined by Dunn (1934, 'Copeia', iv, pp. 167-172). The fundamental units with which we work are individual animals, concerning which assumptions are made. The most important of these are that they possess certain hereditary characters, and that each individual, in life, formed part of a population whose members are connected by protoplasmic interchange. In simple cases the individuals of such a population all resemble one another in certain characters. For taxonomic purposes a selection is made from these common characters, those selected being usually spoken of as having 'taxonomic significance'. The selection is made upon purely empirical grounds and nowadays we have a vast mass of past experience to go upon; in cases where sufficient knowledge is lacking one can only work by analogy. Characters which must obviously be excluded from consideration are those believed not to be

heritable, those subject to direct modification by the environment, teratological characters, and those subject to ontogenetic changes which are not fully known. I am convinced that the characters selected must all be of the same category, for it seems impossible to employ more than one set of criteria in any single system of classification, unless the criteria are themselves inter-related. In the classification of the chemical elements, for example, there is a linear scheme, based upon the atomic structure as reflected by atomic weights. In it, elements of similar structure appear close together, although their chemical properties may be utterly dissimilar. Elements closely similar from a chemical standpoint are widely separated, and it is only due to the fact that there is a periodic relationship between structure and chemical properties which permits the two sets of criteria to be combined into a single two-dimensional classification. This point is mentioned because, although the herpetological system is based upon morphology, there have been attempts to utilize physiological criteria in addition, with results which can only be described as fantastic.

To resume the story of herpetological procedure. When individuals are discovered which differ from other known forms, the first stage is to discover (if possible) whether the points in which they differ have 'taxonomic significance'. If not, the specimens are regarded either as freaks or as being within the normal range of variation. If, however, they differ in characters which experience suggests may be regarded as of taxonomic importance, the next stage is to decide whether the differing individuals and the others together formed part of a single population whose members are connected by protoplasmic interchange. Direct proof, or even good circumstantial evidence, on this point is almost always lacking, and the systematist again has to be guided by experience and analogy. If protoplasmic interchange is unlikely, the differences are usually presumed to indicate at least specific separation.

But if there is no apparent probability of genetic discontinuity, the next step is to discover the proportion of peculiar individuals relative to the rest of the population. If the proportion is low, if they regularly mate with normal individuals, and if both types are known to appear in the same brood, they are classed as a *variety*, *phase*, or *strain*. This may be described and receive a vernacular designation, but scientific names are applied only to whole populations in which the *majority* of the individuals conform to type.

When the number of aberrant individuals increases to such an extent that they form an obvious majority, the population is then *different* from that found elsewhere, though

not necessarily *distinct*. In general, it is these different populations which, subject to certain reservations, receive nomenclatorial recognition as *subspecies* or *races* (the terms are synonymous in herpetology); the intermediate populations do not receive a distinctive name.

The obvious practical difficulty is to determine what constitutes the requisite majority, and it cannot be pretended that there is any uniformity in the matter. At one end of the scale where all individuals of the population in a limited geographical area are alike and there is an abrupt transition to another area containing a different, but equally homogeneous, population, there is no difficulty. But more often there is a slow, ordered, geographical transition between two extremes, with no break in the continuum; here the number of different populations which could be recognized is almost infinite.

It will be noticed that, although in theory subspecific names are applied to populations, a geographical factor comes into our practice. The fact is, that in the laboratory or museum we are not able to tell what is and what is not a 'population'. Populations have certain attributes, amongst them a geographical range. Geographical data are frequently the only ones available to the systematist, and he can only utilize the facts known to him. The consequence is that too much emphasis comes to be laid on this one point and none at all upon others which may be equally or more important. For example:—

(1) A species inhabiting an area of uniform environmental conditions. In one part of its range, suppose, a morphological variant arising out of some genetical change increases until it forms the requisite 'obvious majority'. The population of that area receives a subspecific name. But if the same variant arises and attains numerical dominance *in more than one* geographical area, the resulting populations do *not* receive a subspecific name on the grounds that trinomials are only applied to populations which are different from *all* others. To me this discrimination seems unwarranted.

(2) Again, in very many instances the apparent correlation of races with geographical areas has a deeper, environmental, significance. The morphological differences may be the result of the environment acting directly upon the organism or indirectly by selection of changes originating in some other manner. No matter what the origin of the differences, so long as the differing populations occur in different areas, they will be put in exactly the same subspecific category. If, however, a species occupies two different environmental niches in the *same* area, with a definite variant in each, but connected by intergrades, it is highly improbable that

trinomials will be used, since there will be no geographical correlation.

The invidious recognition by trinomials of certain forms to the exclusion of others, and the rigidity of a system under which infra-specific categories of diverse grades are accorded the same status suggests that the system needs either emendation or rejection. Further progress in the investigation of these infra-specific groups is impossible to the systematist alone, working with the very limited information usually available to him. The most he can do is to indicate the problem and its probable limits; its solution will require investigation along a number of lines, notably ecological and genetical. When more work of that kind has been done we may see the position more clearly, and, with greater knowledge, it may be possible to devise some more satisfactory scheme of classification.

Dr. B. P. UVAROV, F.L.S.:—Entomologists are commonly regarded as narrow specialists spending their lives in describing 'new varieties' of insects differing from each other in a single spot on the wings or in an extra bristle on the legs. There is no doubt that the desire to perpetuate one's name has been responsible for the creation of hundreds of new names that mean very little, but it would not be right to regard all this descriptive work as a waste of time and effort, since it provides extensive data for the study of variation.

In recent years, new tendencies have appeared in entomology with regard to intraspecific taxonomy. In the first place, the idea of subspecies, understood as a geographical race in the sense of ornithologists and mammalogists, proves to be extremely fertile, since it enables a taxonomist to unite numerous minor forms into large species, while preserving their individuality. Studies on geographical variation in insects have already provided many data of interest to biologists in general. For example, it has been found that in some moths there are geographically limited subspecies that do not differ from each other in any external characters, but possess clear and constant anatomical differences in the copulatory apparatus. American tree-crickets (*Oecanthus*) prove to have subspecies differing in nothing but the type of stridulation. Extensive studies on geographical forms of beetles of the genus *Carabus* by Krumbiegel reveal even more remarkable phenomena. In a species distributed over the whole of Europe, more northern races prove to differ from the southern ones not only in trifling external details, but in a number of physiological characters. For instance, there is a scarcely perceptible change in the shape of compound eye from north to south, and parallel with it

goes a change in reactions of beetles to light, so that a species which is nocturnal in the north becomes diurnal in the south. Again, the length of antennæ increases very slightly from north to south, and parallel with this is observed a change in feeding habits; northern races feed on dead animals, while the southern are active hunters for live prey; this is probably due to the increase of the surface area of the antennæ which carries sense organs enabling the insect to find its food.

These few examples serve to confirm the old idea that external characters, however minute, may be only the outward expression of deeply seated causes. This gives a new impetus to the study of small variations in external characters, and modern insect taxonomists are less and less inclined to be 'lumpers', but aim at a complete analysis of variations as correlated with geographical and ecological distribution.

Such studies are still anything but numerous, but their results suggest that causes of geographical variation are far from simple. In some cases there appears to be a direct correlation between change in a certain character and geographical factors (mainly climate), but facts are known when the same character in two allied species varies in opposite directions.

Another point of great general interest emerging from these studies is that isolation of populations of a species often leads to formation of discrete and sufficiently stable taxonomic units. Modern investigations on ecology of insects suggest that relatively few species are distributed really continuously, while the majority are confined to definite habitats and are therefore split up into numerous more or less isolated populations. This is best known in case of insects inhabiting such 'island' habitats as mountain tops, desert oases, etc., but the phenomenon is actually more common, though usually it escapes observation. This kind of variation provides what is named 'microgeographical races' by Dobzhansky who has found mountain races of wild *Drosophila* to differ in nothing but details of chromosome structure.

Further, a great amount of evidence has been accumulated to demonstrate the existence in insects of the so-called 'physiological races'. These are intraspecific groups, identical in structure, but different in their biological characters, such as the preferred food-plant, the annual cycle of development, etc. Since at least some of these physiological races have proved to be genetically fixed, their taxonomic status must be recognized. Their existence shows, again, that evolutionary divergence within a species may commence with deeply seated internal changes, expressed outwardly only in habits, but not in structural variation.

To conclude these, necessarily very brief, remarks, we must admit that even the smallest external differences, if they are not completely irregular and obviously casual, deserve the close attention of taxonomists, because they probably represent quite an advanced stage in variation which begins with internal changes mostly inaccessible for observation, while the external changes lag behind. Their further study should comprise not only morphological, but also experimental, physiological, and genetical analyses, and calls for a close collaboration between taxonomist and his colleagues working in other branches of biology.

The PRESIDENT, in inviting other speakers to take part in the discussion, suggested that just as those working in different branches of biological taxonomy had necessarily different species concepts, instancing palaeontologists, bacteriologists, mycologists, and phanerogamists, so it was probably that intra-specific concepts differed. It was only by attempting to understand practical difficulties that theoretical adjustments could be hoped for.

Professor C. E. McCLUNG (Visitor) :—To a cytologist who, in his studies of germ-cell development, sees a mechanism leading always to the production, in some measure, of unlike individuals, the labours of taxonomists who seek for uniformities within groups seem almost awe-inspiring in their daring. Unities among organisms there are and diversities also: and the immediate practical problem is to detect and evaluate them. A perfect taxonomy would represent the sum of all knowledge of any group. Since we are so far from possessing this, it is not remarkable that our present attempts at classification are unsatisfactory. The willingness of systematists to accept every form of evidence, as shown in the present discussion, is a most encouraging sign of progress toward the ideal taxonomy.

Mr. C. E. HUBBARD, F.L.S., drew attention to the fact that the terms subspecies and variety had been used by systematic botanists, and especially by those dealing with the floras of botanically well-known regions, to cover every grade from a slight variation in one character to a well-defined species. He suggested that in the preparation of floras of large tropical areas, our knowledge of which was still imperfect, it was advisable to group together all the variations of a polymorphic species, rather than attempt to give such variants subspecific or varietal names.

Professor F. E. WEISS, F.L.S., expressed his concurrence with several of the speakers who had asserted that in dealing with subspecies and varieties consideration must be given

not only to structural diversity but also, where possible, to genetic behaviour. He referred to the account Mr. Marsden Jones and he had given of the two blue forms of the pimperl (*Anagallis arvensis*). Of these one form agrees in every character except that of colour with the scarlet pimperl and must be considered a mere variety of the same. The other which differs from the scarlet pimperl by the denticulate margin of its petals and the structure of the marginal glands differs also in its genetical behaviour. While the blue colour-variety is perfectly fertile when crossed with the scarlet pimperl the blue form which is structurally different is completely sterile to the typically scarlet species. This second blue form must therefore be regarded as a subspecies and should be known as *Anagallis arvensis* ssp. *foemina*. (Further particulars are to be found in Proc. Linn. Soc. 1937-38, pp. 146-155.)

Dr. JULIAN S. HUXLEY : It is clear that speciation (taxonomic differentiation) may take place in several ways in the same group, and also may differ radically in different groups. The concept of subspecies has proved its value in birds and mammals, and is now being extended to lower vertebrates and insects. As generally employed in these groups, it involves the following main points : (1) geographical replacement ; (2) frequently, but not always, partial discontinuity. A subspecies is, therefore, a natural or 'real' taxonomic unit, in the sense that it is a self-reproducing group with a characteristic geographical distribution, distinguished from other similar groups by measurable character-differences which can be determined on any reasonably-sized series. Where genetic analysis is possible, it is interfertile with adjacent subspecies of the same polytypic species or Formenkreis (though not necessarily with remote members of the same Formenkreis). This implies that it will often be in genetic interchange with adjacent subspecies.

It has been suggested by other speakers in the discussion that subspecies are purely arbitrary units, and that they always represent a stage in the differentiation of full species. Neither of these contentions would appear to be accurate. To take the latter point first, a frequent characteristic of specific populations of large continental areas is to be broken up into well-marked subspecies which intergrade by crossing at their margins. These interbreeding zones are almost invariably narrow, while the subspecies have relatively large ranges over which they exhibit more or less constant characters. Even when there is a cline extending through the area of one or more subspecies, its slope is very gentle within the subspecific areas, but steep across the interbreeding zones.

Further, even when a population is geographically quite isolated, as a land form on an island, genetic exchange will continue between it and adjacent populations by means of chance immigration, provided the distance between them is not too great.

Sewall Wright (1939)* has shown that such conditions, of partial differentiation into areal groups between which some genetic interchange is still occurring, are the most favourable for rapid evolution. It is accordingly probable that a species inhabiting a large diversified area, and differentiated

* *References to Literature cited by Dr. Huxley :—*

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into a number of subspecies between which reasonable intercrossing occurs, will continue to evolve as a polytypic species, without the subspecies differentiating into full species.

The mechanism by which this partial discontinuity comes into being and is maintained appears to be clear in principle, thanks to the theoretical work of Fisher, Sewall Wright, and others, and the experimental work of Timofeeff-Ressovsky. It consists (1) in regional adaptation of populations followed (2) by harmonious stabilization of the gene-complexes (genetic environment) in relation to the main adaptations, and (3) by the consequent extension of range of the populations possessing such stabilized gene-complexes. When the 'biological tension' resulting from differences of environment is sufficient, selection will differentiate the populations adaptively. The automatic selection of favourable modifiers promoting the viability and reproduction of the adaptive characters will stabilize the different regional gene-complexes in different ways, producing a number of distinct harmonious gene-combinations. Where these intercross, the harmoniously stabilized types will have a selective advantage over the intermediates and recombinations, with their consequent restriction to a narrow 'zone of intergradation'. The result will be a definite but partial biological discontinuity between the groups (subspecies).

Thus, to revert to the first point, we find that subspecies are not necessarily of an arbitrary taxonomic nature, but frequently represent a special stage of equilibrium in the differentiation process—namely, that of partial discontinuity. Although obviously there will exist all gradations between species and subspecies, the intermediate 'difficult' cases will be relatively much fewer than would be the case if subspecies were purely arbitrary.

Thus both species and subspecies are natural groups, in the sense not only that they exist as self-reproducing, geographically delimited, and phenotypically characterized populations, but that they often have certain biological peculiarities. Whereas species are the lowest group-category between members of which fertile interbreeding either is impossible or normally does not occur, subspecies are frequently characterized by what I have called partial discontinuity, this representing a favoured equilibrium-position in taxonomic differentiation. When the biological isolation of subspecies is complete or nearly so, this type of equilibrium is not attained, and subspecies then do represent merely stages in divergence which are not sufficient to merit specific rank.

Mr. Hinton stated that subspecies tend to be graded in their characters in relation to climatic gradients, and thus to fall on what I have called clines (Huxley, 1938). Here

again this appears to be only part of the truth. In the first place, some adaptive modifications, e.g. of colour to background, as in some desert *Peromyscus* (Dice & Blossom, 1937), are not correlated with broad environmental gradients. Secondly, Sewall Wright (1939) has shown that in small isolated populations purely accidental non-adaptive mutations and recombinations will accumulate, so that some diversification is purely an effect of isolation. Thus the differentiation of geographical subspecies may be of different types: (1) non-adaptive, due to relatively complete isolation on small areas; (2) adaptive, (a) non-graded, (b) graded.

A consequence of the Sewall Wright effect is the much greater degree of differentiation seen in isolated habitats (archipelagoes, lake-systems, mountain-tops) than in corresponding areas of continuous habitats (Miller, 1909; Kramer & Mertens, 1938).

Sometimes, as in some island lizards, some fish (Schmidt, 1918), sedentary desert grasshoppers, etc., every colony will have its own characters. In such cases, the term micro-subspecies (micro-geographical race, Dobzhansky, 1937) may be used; but it would seem inadvisable to incorporate the names of such units in the nomenclature as quadrinomials or otherwise.

In addition to geographical subspecies, it seems clear we must recognize ecological and genetic subspecies. Ecological subspecies may be isolated by being confined to different habitats within the same geographical region (e.g. woodland and open country subspecies of *Peromyscus*, Dice, 1931; subspecies of birds in different altitudinal zone, Dementiev, 1938), or they may be what are usually called 'physiological races', confined to a particular host or food-plant (Thorpe, 1939).

In physiological subspecies especially, their morphological distinctions may be very slight or even absent, which renders them awkward material for the museum taxonomist. None the less, they are infra-specific groups which must take their place in the natural system, and can do so only under the title of subspecies.

The same is true of genetic subspecies, which differ generally in structural chromosomal changes and sterility genes. The two 'races' of *Drosophila pseudo-obscura* show us genetic isolation in process of producing true species (discussion in Dobzhansky, 1937).

A complication may occur through a species being differentiated first ecologically and then geographically: e.g. it may comprise numerous physiological races which all show geographical variation. In such cases there seems no logical escape from a quadrinomial system with (ecol.)

and (geogr.) in brackets after the respective subspecific names.

Mr. Wilmott has rightly contrasted the type of infra-specific variation concerned with subspecies with that concerned with the sporadic or regular appearance of variants dependent upon one or a few genes within a population. One is a group-phenomenon, the other an intra-group phenomenon. The former is of the same type as species-formation, the latter not.

If the term *variety* is to be used at all, it should be restricted to the intra-group phenomena. Owing to the numerous and often contradictory senses in which the term has been used, it would, however, be best to abandon it altogether, using e.g. *paramorph* for a non-committal term to denote all variants from the normal, and aberration, mutant, phase, (or in some cases form) for the well-marked intra-group variants. Such variants further should not receive names subject to the international rules of nomenclature, leaving trinomials reserved for group-variations of 'subspecific' nature. Ford (1939) has lucidly summarized the distinction between true polymorphism, depending on a selective balance between sharply contrasted types, and the sporadic appearance of aberrations due to mutation-pressure and chance recombination. It would be interesting to analyse the blue pimpernel described by Prof. Weiss in this discussion, to discover what selectively-balanced agencies operate to keep its numbers maintained.

Clines, on the other hand, are group-phenomena, though of a rather different nature from species and subspecies. They may be combined with true polymorphism, e.g. by the proportion of two phases varying geographically in a regular manner (e.g. the bridled and 'normal' varieties of the guillemot, *Uria aalge*, Southern, 1939; the black and grey phases of the brush opossum, *Trichosurus vulpecula*, in Tasmania, Pearson, 1938).

The term cline is intended as a purely descriptive term, to denote observed gradations in nature, whatever their theoretical explanation may be. In this respect it is superior to other terms such as *Mischzone*, employed by Stresemann to describe such cases as that of the gradation between the pale- and dark-breasted forms of the nuthatch, *Sitta caesia*, across central Europe (see Løppenthin, 1932), since this implies a particular theory of origin and so begs certain important questions (e.g. whether, as the term *Mischzone* implies, the gradation is due to the interbreeding of two types which originally differentiated in separate areas and only met again as a result of migration, or to adaptive differentiation *in situ*, the colour-characters being the external non-adaptive

correlates of the internal physiological adaptations to a climatic gradient).

Again, the term *Sippe* proposed by Reinig (1938) has a purely hypothetical meaning, as a collection of infra-specific groups all phylogenetically derived from the population inhabiting a single centre of distribution during the Ice-age, and each most closely related to that group whose area lies next to it in the direction of the (hypothetical) centre of distribution.

On the supposition that we can accurately delimit such collections of infra-specific groups and their glacial centres of distribution, we shall then, according to Reinig, be able to demonstrate clines running in the direction of their post-glacial migrations. But the phylogeny is merely deduced, and so are the areas of glacial distribution, the post-glacial migration-routes, and the genetic-selective mechanism by which such migration is supposed to result in clines. The clines, on the other hand, are empirical facts, in the shape of gradations in measurable characters, and the conferring of a special term upon them is intended merely to focus attention on this type of taxonomic fact, and to make it easier to describe it succinctly.

By adding prefixes, certain additional facts may be indicated and, in addition, tentative suggestions as to explanation put forward. For instance, *geocline* would denote a cline extending over considerable distances, and *prima facie* correlated with broad climatic gradients; *ecocline* a less extensive cline, apparently correlated with differences in ecological habitat; and *genocline* a usually short cline, not apparently correlated with any environmental gradient, and often bearing traces (recombinations, excessive variability) of being due to crossing between two distinct and originally separate groups or to gene-flow between two harmoniously-stabilized gene-complexes. Such terms, however, are intended as supernumerary, and for any taxonomic use the purely descriptive and non-committal term cline should be employed.

As to how the term should be employed in taxonomy, the following suggestions are made:—

- (1) Taxonomic specification by clines as an *addition* to the ordinary taxonomic practice of specification by named areal group.
- (a) External (inter-group) clines. When a number of subspecies show clines in the mean values of certain characters, the description of these clines should be added after the description of the subspecies. E.g. 'A cline in increasing size to the N. connects subspecies P.x.a., P.x.b., and P.x.c.; a cline in increasing lipochrome coloration to the WSW.

connects subspecies P.x.d., P.x.b., and P.x.e.' When less steep internal (intra-group) clines for the same characters, running in the same directions, also exist within the separate subspecies, this fact can be added at the same time, as can the existence of steep clines at the margins of subspecies which intergrade. It should further always be added whether all the diagnostic characters of the various subspecies are subsumable under the head of the clines, or only some. For in some cases external clines for different characters run in different directions (cf. Miller, 1931, on North American shrikes of the genus *Lanius*) and in other cases, notably with small isolated populations, we may presume that the Sewall Wright effect of accidental (non-adaptive) differentiation may affect some characters, while others show a regular (presumably adaptive) cline. Thus the size of the insular subspecies of wrens (*Troglodytes troglodytes*) in NW. Europe shows a regular cline (Salomonsen, 1933), while in their markings they are not so regularly graded.

Such specification constitutes an additional and very succinct description of variation within the species as a whole, but does not itself constitute a part of taxonomic nomenclature.

- (b) When only internal clines are known, they should be added after the description of each individual subspecies. They may throw light on selective processes in operation in nature, and point the way towards the detection of external clines running in the same direction. Here, again, clines constitute only an additional method.
- (2) Taxonomic specification by clines as a *substitute* for specification by named areal groups. This will be necessary (a) when a population shows a regular and gradual change, with no sharp breaks or changes of slope, over a considerable area, as in the case of the nuthatches above referred to. Løppenthin (1932), in describing this case, proceeds to allot three subspecific names to what on his own showing are merely arbitrary stages in this gradation, besides the two subspecies constituting its end-terms. This must be regarded as incorrect taxonomic practice, since the designation of subspecies should only be given to groups which are relatively constant over a recognizable area of distribution, and are visibly distinguishable, in not unreasonably long series of specimens, from neighbouring groups. To use the same term also for mere

stages in a continuous series is both illogical and confusing.

It is accordingly suggested that clines can here be used as part of the primary taxonomic description, by stating that between P.x.a. and P.x.b. (the end-terms of the gradation) a cline exists; its nomenclature would then be 'cline (abbreviated cl.) P.x.a-b.' As these end-terms will have already been described, and their areas of distribution specified, nothing further is needed. If desired, however, arbitrary stages within the cline can be denoted by Roman numerals or letters.

In the case of the nuthatch, the two end-terms appear to be true subspecies, in that they are relatively constant in type over a considerable area. Other cases might present themselves in which the cline was continuous to either end of the range of the species. In such cases, it would seem undesirable to describe the end-terms as separate 'subspecies': a double (hyphenated) trinomial, prefixed by the abbreviation cl., should be conferred on the cline as a whole, and the end-terms referred to, if necessary, as forms *a* and *b* of cl. P.x.a-b.

- (b) Specification by clines is also desirable so long as we are uncertain whether a general gradation consists of a number of true, distinguishable subspecies or of a continuous internal cline. Further collecting may show that subspecific naming is actually required; in that case it can be substituted for specification by a cline between two named end-terms, and the cline becomes merely an external cline, supplementary to standard taxonomic practice instead of itself forming a taxonomic unit. So long, however, as there is any doubt in the matter, it is inadvisable to confer subspecific names, which, if they later proved not to be required, will continue to cumber the nomenclature and to confuse the real issue.

An excellent example is provided by Thomas and Wroughton's paper (1916). Here seven 'subspecies' of *Callosciurus sladeni* are described from nine stations along 250 miles of the E. bank of the Chindwin River. On analysis, it appears that what really exist are two clines, separated by the largest tributary on the E. (rivers here appear to act as effective isolating agents, since the genus is represented on the W. banks of the Chindwin by a quite different species). The southern cline is from grey to rufous (N. to S.), but need not claim our detailed attention, since collections

were only made at three stations in 110 miles, and for each collection a new subspecies is erected! The other cline is a very regular one from grizzled brown to very pale (N. to S.). Collections were made at five stations in 85 miles. Four subspecies are named, and at one station the population is described as intermediate!

Here we have the fact of great interest that clines can behave as taxonomic units in having their range limited by geographical barriers. There would appear, however, to be no valid reason for giving subspecific names to any but the end-terms of each cline (or preferably a hyphenated trinomial to the whole cline, which in this case would be designated cl. *C. shortridgei-harringtonii*), until it is ascertained whether (though this seems *prima facie* unlikely) there are any real breaks within the two gradations.

Ecological clines such as those described by Gregor (1938) for *Plantago maritima* or suspected by Rensch (1934) for land-snails might perhaps be dealt with in the same way, but it would seem preferable to avoid incorporating them in the nomenclature, since they will be repeated, often with variations, in numerous localities.

SUMMARY.

(1) Subspecies may represent merely stages in specific differentiation.

(2) In many cases, however, they represent an equilibrium-position of partial discontinuity, brought about by local adaptation to different conditions within the range of a continuous population, followed by the harmonious stabilization of the gene-complexes in relation to each main adaptation, and consequent restriction of the zones of intergradation.

(3) The term *variety* has been used in so many different senses that it should be abandoned. Some neutral term like *paramorph* should be employed to cover any variant differing from the normal.

(4) Two types of taxonomic differentiation should be distinguished—group-differentiation, leading to the formation of subspecies and species; and intra-group differentiation, leading to the appearance of sporadic aberrations or forms, or of true polymorphism, in which sharply-contrasted types are maintained in considerable numbers within a population, owing to selective balance.

(5) Character-gradations or clines constitute another type of group-differentiation. In most cases, clines should be used only as an auxiliary method of taxonomic description, but

cases occur where a named cline should form part of the nomenclature. It is suggested that the names of such clines should consist of the hyphenated names of the two end-terms, prefixed by the abbreviation cl., the end-terms themselves not to form part of the nomenclature unless constituting true subspecies.

Dr. R. MELVILLE, F.L.S. :—There are a few points I should like to raise, some of which have a bearing on what Prof. Huxley has just said and in certain respects are supplementary. We are told that hybridization is, in general, of rare occurrence among animals, but the reverse is the case among plants, at least in certain groups. The genera *Ulmus* and *Salix* may be cited as examples. In such genera many of the species are connected by an intergrading series of hybrid forms. Clines in Huxley's sense, i.e. based on a gradation of characters over the geographical range of the species, may occur also. The hybrids occur sporadically over the joint range of their parent species, but nevertheless they can be arranged in sequences that are tantamount to clines by using such characters as leaf-shape, and indumentum in which intergrading occurs. These sequences are without any geographical basis.

It does not appear to be desirable to give names to many of the forms constituting such hybrid sequences, and it would, in fact, be advantageous to invent an entirely new term to describe hybrid forms. This procedure would avoid the use of the much abused term 'variety' and help to clarify the position with respect to its use.

PROF. W. GARSTANG, F.L.S., remarked that in marine animals the local variation was often gradational, in the sense that the average number of vertebrae, fin-rays, etc., goes up or down with the gradient of salinity or temperature. Thus in passing from the Baltic to the Atlantic through the North Sea herrings show a continuous increase in the average number of vertebrae, and this runs parallel with a steady increase in the salinity. It is possible that this relation is a consequence of the direct influence of the environment on growth. In the mackerel an American subspecies can be distinguished from the European by a marked difference in the average number of spots among the bars on the sides of the fish, although individuals can be picked out which are precisely alike. In this case the variation curve would be bicuspid if equal samples from both sides of the Atlantic were mixed; while the curves for each subspecies separately would be simple, but with different modes. It is not easy in this case to think of this difference as directly environmental. It is correlated with what is practically a discontinuity in the area of distribution, i.e. isolation.

PROCEEDINGS OF THE GENERAL MEETING**16 February 1939.**

Mr. J. RAMSBOTTOM, O.B.E., M.A., Dr.Sc., President,
in the Chair

The Proceedings of the General Meeting held on Thursday, 2 February 1939, having been circulated, were taken as read and confirmed.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

Certificates of recommendation of the following candidates for Fellowship were read :—For the second time, in favour of Debabrata Chatterjee, Balai Chand Kundu, Walter Samuel Millard, and Joseph Burt Hutchinson.

The President reported the deaths of the following Members :—Prof. J. W. Carr, Dr. E. J. Collins, Mr. J. W. Bodger, and Mr. Daniel Finlayson, Fellows of the Society ; Prof. Carl Schroeter, Foreign Member.

The Meeting considered the two motions before it regarding National Parks, the one drafted by the Society's Officers, the other by Dr. Julian S. Huxley :—

1. The Linnean Society of London accepts the definition employed in the African Fauna Convention as an ideal for the preservation of Nature ; but it knows that the term ' National Park ' has been given to areas which for various reasons are unsuitable for inclusion within the definition,—e.g. too limited or situated too near populated areas. For such it recommends the setting apart within each Park of special nature reserves under proper control ; and it would like all authorities with power over Parks to be able to command advice from such bodies of naturalists as are competent to give it.

2. The Linnean Society of London agrees that a National Park may be defined as a relatively large area of unspoilt or wild country, nationally dedicated to the purposes of (1) the preservation of the scenery, (2) the conservation of the plant and animal wild life, and other features of natural interest, (3) the enjoyment of these various features by the general public.

The absolute size of a National Park will vary according to circumstances, as will the relative emphasis on its second and

third main functions. In a small or densely populated country the size of National Parks will be smaller, and more emphasis will be laid on public access, while less can be done for the preservation of wild life. Neither function, however, can be neglected. Even in the most densely populated country undue interference with natural features or wild life must always be avoided, and absolute sanctuaries for wild life should be provided within National Parks wherever possible. Similarly, even in the wildest and least developed countries, reasonable public access must be provided to large portions of any National Park.

The Society would like all authorities with power over Parks to be able to command advice from such bodies of naturalists as are competent to give it.

Dr. W. T. CALMAN stated that he desired to propose the resolution drafted by the Society's Officers subject to an alteration, namely that the word 'seek' be substituted for the words 'able to command' in the last sentence.

Lieut.-Col. R. B. SEYMOUR SEWELL seconded the proposed alteration.

Dr. G. S. CARTER proposed that the words 'as absolute sanctuaries for wild life', which occur in Dr. Huxley's motion, be substituted for the words 'under proper control'.

Mr. H. R. HEWER seconded this.

Prof. T. G. B. OSBORN pointed out that to make an area in Australia such as the Belair National Park an absolute sanctuary for wild life would protect the invading rabbits.

Mr. M. A. C. HINTON spoke on behalf of Dr. Huxley's motion, laying emphasis on the undesirability of accepting a definition, as in the Officers' motion, without more precisely quoting it. He suggested that the first paragraph of Dr. Huxley's motion might replace the opening words of the Officers' motion as far as 'preservation of Nature; but'.

Miss M. RATHBONE suggested that the word 'indigenous' be introduced into the expression 'absolute sanctuaries for wild life', reading 'absolute sanctuaries for indigenous wild life'.

Mr. D. J. SCOURFIELD questioned the meaning of the word 'agrees' in the opening sentence of Dr. Huxley's motion.

Prof. F. E. WEISS said that to combine the two motions seemed impossible.

Dr. CALMAN criticized Dr. Huxley's motion and suggested that Mr. Hinton's objection could be got over by making reference to the place of publication of the very words of the definition of the African Fauna Convention.

The PRESIDENT moved from the chair that this be an amendment.

Mr. HINTON said that the motion as amended by Dr. Calman, with this further amendment, would satisfy him.

Capt. C. DIVER supported this.

Dr. G. S. CARTER withdrew his amendment.

The motion in the form thus arrived at (printed below) was put to the meeting and accepted:—

The Linnean Society of London accepts the definition employed in the African Fauna Convention * as an ideal for the preservation of Nature; but it knows that the term 'National Park' has been given to areas which for various reasons are unsuitable for inclusion within the definition,—e.g. too limited or situated too near populated areas. For such it recommends the setting apart within each Park of special nature reserves under proper control; and it would like all authorities with power over Parks to seek advice from such bodies of naturalists as are competent to give it.

* This definition reads as follows:—

'1. The expression "national park" shall denote an area (a) placed under public control, the boundaries of which shall not be altered or any portion be capable of alienation except by the competent legislative authority, (b) set aside for the propagation, protection, and preservation of wild animal life and wild vegetation, and for the preservation of objects of aesthetic, geological, prehistoric, historical, archaeological, or other scientific interest for the benefit, advantage, and enjoyment of the general public, (c) in which the hunting, killing, or capturing of fauna and the destruction or collection of flora is prohibited except by or under the direction or control of the park authorities.

'In accordance with the above provisions facilities shall, so far as possible, be given to the general public for observing the fauna and flora in national parks.' (International Convention for the Protection of Fauna and Flora... London, November 8, 1933. Treaty Series No. 27. London, H.M. Stationery Office, 1936.)

Capt. C. DIVER, F.L.S., gave an account of the scheme for a National Atlas of Britain.

Abstract.—

At the Cambridge meeting of the British Association (1938) a joint committee of various sections was set up at the request of Section E to explore the possibility and desirability of producing a National Atlas of Great Britain and Northern Ireland, or, alternatively, of the British Isles. The biological members of this Committee are Professor A. G. Tansley, F.R.S., and Professor E. J. Salisbury, F.R.S., from Section K, and the speaker from Section D.

The proposed Atlas would aim at a strictly objective and scientific presentation of the physical geography (including geology, climatology, and hydrography), bio-geography, economic geography, and human geography (including prehistoric and cultural geography) of this country.

An enterprise of such scope and importance should be entitled to support from public funds, but its success from a scientific standpoint must depend on scientific workers and scientific bodies willing to undertake responsibility for the accuracy of maps within particular fields. At the present stage of their enquiry the Committee are seeking to ascertain the measure of approval, support, and co-operation which the

project can command. The biological members of the Committee would be glad to receive any suggestions of data of biological interest and already in existence which might suitably be included in the bio-geographical or other sections. On any scheme the number of biological maps must be relatively small, but it is desirable that the best possible use should be made of the space available.

A note containing preliminary suggestions for maps which might be included appears in the current (February) number of the 'Journal of Ecology', to which reference should be made by those who are interested in the scheme. Since this was drafted further suggestions have been received that maps should be included showing the degree of glaciation during the last glacial epoch, the distribution of soil types, climatic factors that are of particular interest to biologists, marine currents and seasonal isotherms, migration routes, isophenes, and nature reserves, sanctuaries, etc. How many of these suggestions can be incorporated depends upon the completeness of the data available and the amount of space allotted.

Rev. J. E. HOLLOWAY, D.Sc., F.R.S. (Visitor), gave a lecture, 'New Zealand Pteridophyta'.

Abstract.—

It is well known to botanists that Pteridophytes play a notable part in the vegetation of New Zealand. *Equisetum* and *Selaginella*, however, are altogether absent.

Of the earlier Mesozoic Fern-families there is a strong representation, including several species of *Gleichenia* and *Schizaea*, *Lygodium articulatum*, three Osmundaceae, and one *Marattia*. In accordance with their modern distribution elsewhere, these ferns are in a few cases restricted in New Zealand to the warmer North Island. Apart from this, however, they are on the whole much in evidence in the usual wet mixed forests. *Gleichenia Cunninghamii*, *G. circinnata*, *Leptopteris superba*, and *L. hymenophylloides*, are all very common in such forests from north to south, and are well known to New Zealanders for their beauty. *G. dicarpa* is a common member of lowland bog associations throughout the country, and *G. alpina* on upland bogs. *Lygodium articulatum* is a high climber in North Island forests, ascending even into the canopy of tall forest-trees.

There are two species of *Ophioglossum*, of which one is very widespread and abundant in a variety of localities, more especially in hill and mountain-side native turf. The one species of *Botrychium* occurs quite commonly in various types of forest and of shrubbery.

In the heavy wet mixed forests there is a luxuriant and varied display of the more modern fern types, to a few of which reference may be made. Tree-ferns are a very characteristic

feature of these forests right down to Stewart Island in the extreme south. Four genera, embracing eight species, are represented in New Zealand, and one species, viz. *Hemitelia Smithii*, is even to be found on the subantarctic Lord Auckland Island. *Cyathea medullaris* and *Dicksonia fibrosa* are noble plants.

The Blechnums and the Hymenophyllaceae are the dominating fern-types. Of the latter family there are in all twenty-five species, viz. *Hymenophyllum* (18), *Trichomanes* (6), and *Cardiomanes reniforme*, most of these, including the last-named, occurring abundantly, usually as epiphytes. Several species of *Hymenophyllum* ascend, in wet forests, into the tops of the forest-trees.

Lycopods are represented by twelve species of *Lycopodium*, two species of *Isoetes* in mountain lakes, and the diminutive *Phylloglossum Drummondii* on the Auckland clay moorlands. Two of the Lycopodiums are fairly common pendulous epiphytes in wet forests. *L. fastigiatum* and *L. scariosum* (comparable to the northern hemisphere *L. clavatum* and *L. complanatum*) occur freely on all mountain sides in open turf associations, and the cosmopolitan *L. Selago* at somewhat higher elevations. *L. volubile* is a very beautiful climber or scrambler in shrubbery, and is commonly used throughout New Zealand for decoration purposes. On the northern moorlands the tropical *L. cernuum* and also *L. densum* are quite abundant. Both of these species are large handsome plants, the erect branches of *L. densum* attaining a height of eight feet or even more when growing in close shrubbery. Three other species belong to lowland bogs. *Phylloglossum* is still to be found throughout the Auckland province, but is steadily becoming rarer as these moorlands come under cultivation.

The two genera of Psilotaceae are each represented by one species. *Tmesipteris tannensis* is a very common pendulous epiphyte, usually on tree-fern trunks, in wet forests throughout New Zealand. It is not very unusual, however, to find it occurring as a short erect plant in patches of humus on the forest floor. *Psilotum triquetrum* is confined to much drier exposed situations in the Auckland province, more especially on the eastern coast-line, and is best known from the volcanic islet of Rangitoto in Auckland Harbour.

Over a period of some thirty years the present speaker has discovered the gametophytes of nine species of *Lycopodium*, and also those of *Tmesipteris* and *Psilotum*, but only one in the case of *Phylloglossum*. Prof. A. P. W. Thomas found numerous gametophytes of *Phylloglossum* nearly forty years ago. The speaker's experience has been that continued field-work is bound to develop in the searcher a facility for recognizing gametophyte localities, and that an appropriate method of soil-sifting (combined with patience) will do the

rest of the job. Moreover, where gametophytes are present, they are quite often in considerable numbers.

The PRESIDENT expressed the pleasure that all members felt at having Professor Holloway with them to give at first hand an account of New Zealand Pteridophytes and of his methods of searching for gametophytes. He called on Sir Albert Seward to say a few words about the paper.

Sir ALBERT SEWARD regretted that there was no time to discuss Dr. Holloway's fascinating account of the New Zealand Pteridophyta. He was glad of the opportunity of saying how greatly British botanists enjoyed meeting their New Zealand colleague and welcoming him to this country. He had always thought most highly of Dr. Holloway's work, and, he added, it had been done in very difficult circumstances, in the course of many years devoted to duties of a different kind. He congratulated Dr. Holloway on his most important discovery of a conducting strand in the gametophyte of *Psilotum*, and expressed the hope that he would form his own opinion of the significance of the discovery, without paying too much attention to the various divergent opinions offered by botanists whom he met during his short visit.

Mr. H. W. PARKER, on behalf of the author, gave an account of Dr. H. E. BRINK's paper 'A histological and cytological investigation of the thyroids of *Arthroleptella bicolor villiersi* and *Bufo angusticeps* during the normal and experimentally accelerated metamorphosis'. (Communicated by Mr. M. A. C. HINTON, F.R.S., Sec.L.S.) [Printed in full below.]

A HISTOLOGICAL AND CYTOLOGICAL INVESTIGATION OF THE THYROIDS OF ARTHROLEPTELLA BICOLOR VILLIERSI AND BUFO ANGUSTICEPS DURING THE NORMAL AND EXPERIMENTALLY ACCELERATED METAMORPHOSIS.

By H. E. BRINK, D.Sc., Department of Physiology,
University of Stellenbosch, South Africa.

(Communicated by Mr. M. A. C. HINTON, F.R.S., Sec.L.S.)

ALTHOUGH the subject of amphibian metamorphosis and its relation to the thyroid has during recent years been studied very exhaustively, and with a fair amount of success, by numerous investigators, quite a number of problems in connexion with this established relationship still remain to be solved. The object of this investigation was an attempt to solve some of these problems. In South Africa, and especially in the Cape Province, are to be found a number of species of *Anura* with a normally abbreviated metamorphosis. Instead of the usual three to four months needed for growth

and differentiation (from the fertilized ovum up to completion of metamorphosis), these frogs only take from seven to ten days for the whole series of changes from the egg to the adult form. One such species, viz. *Arthroleptella bicolor villiersi* was collected in Jonkershoek, Stellenbosch, and used for this investigation. *Bufo angusticeps*, a species with the normal 3-4 months' metamorphic period was used for comparison.

The *Arthroleptella* material was classified into seven diagnostic metamorphic stages and compared with similar stages in the life-history of normal *Bufo* and of *Bufo* undergoing accelerated metamorphosis by treatment with thyroxin and anterior hypophysis extract respectively. The usual staining methods were used for the general histology of the thyroid, whereas the Koletchev (Nassonov modification), Mann-Kopsch, Kraus, and Bensley methods were employed for the Golgi-apparatus and for the cytology generally. Quantitative determinations were also made of the body volume, thyroid volume, and colloid volume respectively.

Comparative histology of Arthroleptella and Bufo thyroids during diagnostic stages of the metamorphosis: (1) *Epithelium*: During the pro-metamorphosis (Etkin, 1930) there is a steady increase in the height of the follicular epithelium which reaches a maximum at the beginning of the metamorphic climax. Towards the end of the climax in both species, there is a sudden decrease in epithelial height, which reaches a minimum in the adult animal. In *Bufo* this minimum is of the same value as at the beginning of the pro-metamorphosis, but in the case of *Arthroleptella* it is much lower. The maximum is higher for *Arthroleptella* than for *Bufo*, viz., 12.75μ as against 9μ . It is therefore concluded that the epithelium is much more active during the pro-metamorphosis in *Arthroleptella* than in *Bufo*.

(2) *Colloid*: The total amount of colloid present during all stages in *Bufo* far exceeds that in *Arthroleptella*.

(3) *Vacuoles*: The number of vacuoles in the colloid is much greater in the *Arthroleptella* thyroid than in that of *Bufo*.

(4) *Blood-supply*: In *Bufo* the blood-supply is very weak during the early stages; at the beginning of the metamorphic climax it suddenly increases, reaches a maximum, and then declines to its minimum in the adult animal. In *Arthroleptella* the blood-supply is very profuse during the whole of the metamorphic period, only decreasing after the metamorphosis has been completed and reaching a minimum value in the adult animal.

The histology of the Bufo thyroid during the accelerated metamorphosis resulting from thyroxin treatment: The thyroids of the thyroxin-treated larvae show throughout all the

stages of the metamorphosis a functional repression clearly indicated by (a) low epithelium, which at no stage reaches a value comparable with that of the controls; (b) colloid, which shows definite signs of ageing and of change of composition, due, no doubt, to the fact that there has been no renewal, and (c) blood-supply, which is very weak throughout the whole period. A characteristic phenomenon observed in these thyroxin-treated thyroids is what we have called 'follicle-fusion'—two adjacent follicles fusing to form one large follicle. This is due to a reduction of epithelium.

These results are in complete accord with those of Clements (1932), Uhlenhuth and Schwarzbach (1927) and Leo Loeb (1929), although none of these investigators mention that they observed any 'follicle-fusion'.

The histology of the Bufo thyroid during the accelerated metamorphosis following hypophysis treatment: The first and most obvious result of hypophysis treatment of the *Bufo* larvae is an immediate increase in the growth and differentiation of the thyroid. Another effect is the enormous hyperplasia which also starts immediately on commencement of the treatment. Nearly all investigators in this field lay great stress on this characteristic hyperplasia (Uhlenhuth and Schwarzbach 1924: Zurawski and Uhlenhuth 1932: Paal 1931: Adams 1932: Loeb and Bassett 1929: Aron, 1930, etc.). The third and chief result is an intense vacuolization of the colloid especially during the beginning of the metamorphic climax. That this intense vacuolization indicates an excretion of colloid into the blood-stream seems fairly obvious and is also contended by most of the investigators previously mentioned.

The quantitative relationship of body-volume, thyroid-volume, colloid, and epithelium during the normal and accelerated metamorphosis: (1) *Bufo* and *Arthroleptella* (normal): (a) the relative size of the thyroid is in both cases more or less the same.

(b) The maximum is reached in both cases at the beginning of the metamorphic climax.

(c) After the metamorphic climax the thyroids of both decrease in size and reach a relative minimum in the adult animal.

(d) The colloid relations differ very much in the thyroids of the two species. In *Bufo* the colloid value increases steadily and reaches a maximum shortly before the metamorphic climax, when it suddenly decreases, which shows an excretion into the blood-stream. In the case of *Arthroleptella*, however, the relative colloid volume is very low during the whole metamorphic period. Only towards the end of the metamorphic climax is there a sudden increase which reaches

a maximum at the end of metamorphosis and remains more or less constant at this figure throughout adult life. This undoubtedly shows that the amount of colloid secreted during the early stages of the metamorphosis is more or less equal to the amount excreted into the blood-stream, so that at no period during the process is there any intrafollicular accumulation of colloid.

(2) *Bufo*—*accelerated metamorphosis*: (a) *thyroxin-treatment*: The absolute and relative thyroid volumes remain low in comparison with those of the controls confirming the histological findings, viz. a general functional repression.

(b) *Hypophysis treatment*: In the early stages there is a great increase in the thyroid volume, which, however, suddenly undergoes, at the beginning of the metamorphic climax, a great decline corresponding to the excretion of large quantities of colloid from the follicles as shown in the histology. The hyperplasia which takes place *pari passu* with this excretion compensates to a certain extent this volume decrease.

Summary.—From the results obtained in this series of studies it is clear that the thyroid must be considered as the chief causal factor in the metamorphosis of *Anura*. From the microscopical investigation, volume determinations, and cytological study the following conclusions have been drawn:—

(1) The thyroid activity increases shortly before the metamorphic climax, as indicated by an increase in epithelial height, volume increase, and increased vascularity.

(2) In the case of the *Bufo* thyroid there is an accumulation of colloid in the follicles until shortly before the climax. During this latter stage, the accumulated colloid diminishes in amount, but again rises to its former maximal level after metamorphosis has been completed. In the case of *Arthroleptella*, on the other hand, there is no such colloid accumulation before the metamorphosis. The maximum amount of colloid is only found in the follicles after the metamorphosis has been completed. This difference is interpreted as showing that in *Bufo* the colloid is only excreted into the blood-stream at the beginning of the climax, whereas in *Arthroleptella* colloid secretion and colloid excretion run parallel courses throughout the metamorphic period.

(3) The position of the Golgi-apparatus in the follicle-epithelium of the Anuran thyroid cannot be taken as an indication of the excretion-polarity as asserted by Cowdry (1922) and others. This contention is in agreement with the findings of Hirschlerowa (1927), Ludford and Cramer (1928), and Uhlenhuth (1934). Not for a single cell could a basal position of the Golgi-apparatus be demonstrated, showing

conclusively that this protoplasmic constituent cannot be used as an indication of basal excretion.

(4) The Golgi-apparatus stands in relation to the secretory activity of the epithelial cells. During increased activity of these cells the Golgi-apparatus assumes a thickened, U-shaped, doubly refracting form, while in the resting or exhausted condition it floats about the cytoplasm in the form of thin, short, rod-like structures (Nassonov, 1923, 1924 : Krogh, Linberg, and Okkels, 1932 : Okkels, 1932 : Uhlenhuth, 1934).

(5) Thyroxin treatment represses the normal activity and differentiation of the thyroid in Anuran larvae, so that they show, before, during, and after metamorphosis a tendency to resemble the thyroids of controls at an earlier stage of development.

(6) The hypophysis treatment first stimulates the growth and differentiation of the Anuran thyroid and later leads to an evacuation of the accumulated colloid by a process of absorption preceded by a liquefaction of the colloid into a chromophobe or unstainable form. This liquefied or chromophobe colloid is then excreted, in some way at present unknown, into the blood-stream.

(7) In *Arthroleptella* shortly before the metamorphic climax definite intercellular excretory canaliculi can be clearly seen. The only other investigator who has since seen these or similar canaliculi is Hirschlerowa (1927), who gives the following explanation for their presence with which I am in complete accord :—' Für den Weg, auf welchem das sich im Drüsenbläschen bildende Kolloid dem Organismus abgegeben wird, halte ich interzelluläre Kanälchen (Ausführungskanälchen), die das Azinuslumen mit den interazinären Lymph- und Bluträumen verbinden und während der Metamorphose in grösserer Zahl auftreten.'

The full text and accompanying illustrations of the investigations on which the above résumé is based are to be found in the 'Annals of the University of Stellenbosch', XIV, ser. A, no. 1 (Aug. 1936), pp. 1-111, figs. 1-27. Original title in Afrikaans : Die Skildklier en Metamorphose by die Amphibia.

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PROCEEDINGS OF THE GENERAL MEETING

2 March 1939

Mr. J. RAMSBOTTOM, O.B.E., M.A., Dr.Sc., President,
in the Chair

The Proceedings of the General Meeting held on Thursday, 16 February 1939, having been circulated, were taken as read and confirmed.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

The following candidates, whose names were read for the third time, were balloted for and elected Fellows :—Charles Russel Metcalfe, M.A., Ph.D., Alice Mary Geldart, Mohammad Sayeedud-Din, M.A., B.Sc., Clarice Vivian, Leonard Richmond Wheeler, B.A., M.Sc., Ph.D., John Frederick Gustav Chapple, Major Albert Pam, O.B.E., Joseph Burt Hutchinson, M.A., Walter Samuel Millard, Debabrata Chatterjee, M.Sc., and Balai Chand Kundu.

The President announced that five vacancies existed in the list of Foreign Members, due to the deaths of Prof. W. M. Wheeler, Prof. C. Raunkiaer, Dr. A. Zahlbruckner, the Abbé V. Grégoire, and Prof. C. Schroeter ; he also reminded the Society that the time was approaching for the nomination of Members of Council for next Session and for the selection of the Linnean Gold Medallist. He asked that Fellows wishing to put forward names for consideration by the Council should forward them in writing to any of the Secretaries.

The following exhibits were shown, in addition to those described in the communications below :—

DEPARTMENT OF BOTANY, BRITISH MUSEUM (NATURAL HISTORY).

- (a) Drawings of Plants by Miss BEATRICE CORFE.
- (b) Miniature models of plants in painted 'brass and other metals', by Miss BEATRICE HINDLEY.

Sections of the wood of *Bursera fragrantissima* Bullock, prepared by Mr. C. R. METCALFE.

A new species of *Monostroma* from New Zealand, by Dr. V. J. CHAPMAN.

A double symbiosis between a coral, a hydroid, and an alga, by Capt. A. K. TOTTON, M.C.

The coral, a flexible coral or Gorgonian, *Anthoplexaura dimorpha*, from Japan, anaesthetized before fixation to show the expanded polyps. A commensal hydroid, *Hydrichthella epigorgia*, growing round the bases of the polyps, can be seen with a lens. The association is a constant one. There is an alga associated with the hydroid so that here we have a case of double symbiosis.

Heteroxenia fuscescens (Ehrenberg) from Ghardaqa, Red Sea, by Capt. A. K. TOTTON, M.C.

The Red Sea fauna includes ten Xeniids, remarkable for their large non-retractile tentacles. The tentacles of *Hetero-*

xenia species are all pulsatile, and the larvae are retained on the surface of the colony between the siphonozooids, small reduced polyps that only appear periodically at the breeding season, and have functions in connection with control of water-content of the coelenteron.

TURTLES STRANDED ON THE BRITISH COAST, 1938-1939.

BY MR. H. W. PARKER, M.A., F.L.S.

THE extraordinarily large number of turtles stranded on the British coast during the period from November 1938 to January 1939 has aroused some interest on account of the suggestion that records of the distribution of these reptiles might be of assistance in studying ocean currents (Deraniyagala, 1938). The author (1939) suggested that, if this hypothesis is tenable, the events of 1938 might indicate that there had been an inflow of Atlantic water into the English Channel, but Russell (1939) is doubtful whether this has really occurred; as an alternative he suggests that there is evidence of a northerly movement of warm water in recent years which may have brought these turtles within the zone of westerly winds which would drift them into the Channel.

Since the letters referred to were written, the author has had an opportunity of examining some of the specimens and the more precise knowledge thus obtained alters the circumstances. Previously it was believed that all the specimens were Atlantic Loggerheads (*Caretta caretta* Linn.), and, since this species occurs on both sides of the Atlantic Ocean, Dr. Russell's suggestion had much to recommend it. But now it seems more probable, though not by any means certain, that the turtles have crossed from the American shore. The actual records for the winter of 1938-39 are as follows:—

I. *Atlantic Loggerhead, Caretta caretta* (Linn.). (i) Selsey Bill, Nov. 18th. (ii) Felpham, near Bognor, Dec. 11th. (iii) Tenby, Dec. 11th. (iv) Bognor, Dec. 16th.

II. *Kemp's Loggerhead, Caretta kempi* (Garman). (i) Beaumont, Jersey, Dec. 10th. (ii) Portreath, near Redruth, Dec. 30th. (iii) Pagham, near Selsey, Jan. 28th.

III. *Unidentified* (specimens destroyed). (i) St. Ives, circa Nov. 10th. (ii) Bexhill, Dec. 11th. (iii) Near Lyme Regis, Dec. 18th.

Whilst the first-mentioned species is known to occur on both sides of the Atlantic, Kemp's Loggerhead is generally

believed to be an essentially American species, ranging from the Gulf of Mexico northwards, occasionally to the coast of Massachusetts; it has been recorded recently from the British Coast (Deraniyagala), but there is no record of it from the tropical or subtropical waters of the Eastern Atlantic. If the known distribution is correct, it is obvious that these turtles must cross the Atlantic, presumably in the Gulf Stream and West Wind Drift, and it is interesting to try to discover the reasons which have led to their being carried so far afield.

The rate and direction of flow of the currents of the North Atlantic are known to be variable, and sufficient information is not available for calculations of the time which would be necessary for the animals to be carried over as passive objects. From Schmidt's work on the breeding of the eel it is apparent that the journey-time for the larval eel is in the neighbourhood of two years. These larvae are relatively feeble swimmers and, being totally submerged, are not subject to wind-action, features in which they differ markedly from turtles. Another line of attack on the question of the probable length of time occupied in the crossing is furnished by a study of the movements of derelict ships. No single derelict is known to have made the complete journey from the Gulf of Mexico to the British coast, but a composite time derived from sections of the journeys of two such objects can be calculated. The *Fannie Wolston* was in $29^{\circ} 25' N.$ by $76^{\circ} 52' W.$ (approx.) on Feb. 14th, 1894, and was reported on 10 October of the same year in about $38^{\circ} 48' N.$ by $62^{\circ} 30' W.$; the *W. L. White* passed close to the latter position in the early part of April 1888, and was finally washed ashore in the Hebrides on 23 January 1889 (Krümmel, 1911). Thus the time from a position just north of the Bahamas to the British coast is approximately seventeen and a half months. There is reason to suppose that the time taken by a turtle would be less than this, since swimming has to be taken into account. There is no suggestion that the turtles deliberately swim eastwards; they are obviously 'lost' or they would never have appeared on the British coast. Under the circumstances, lacking any migrational or homing directional influence, movement might be expected to be random, with a resultant of zero. But the wind and the run of the sea must be taken into account. It is well known that surface vessels are considerably retarded by wave action when meeting a head-sea, but assisted by a following sea; consequently random swimming movements by a turtle (which necessarily spends much time on, or close to, the surface, in the region of prevailing westerly winds will produce an easterly resultant movement. In addition, it is highly probable that the turtles exhibit a preference in the

matter, and would elect to travel comfortably with the seas rather than be severely buffeted in trying to swim to the westward, against them. A journey-time of considerably less than $17\frac{1}{2}$ months is thus to be expected and it is more probably in the region of 13-14 months. If this estimate is correct, it follows that the turtles which appeared off our coasts in November and December must have taken their departure from the American shore about September or October 1937. It may be significant that September is the worst hurricane month in the Caribbean region, and it seems possible that the turtles are started upon their involuntary journey by some violent but local storm of this nature rather than by any major change in the flow of the ocean currents.

Some support for the idea that the turtles do actually accomplish this lengthy journey is to be found in the fact that all the turtles which have been recorded from the British coast (Luth, Hawksbill, Atlantic, and Kemp's Loggerheads) are carnivorous. The Green Turtle, which is largely herbivorous and would be unable to find food during an ocean crossing, is the only one of the turtles inhabiting the western Atlantic which has not been found on our coast. It has, it is true, been reported from the Dutch and Belgian coasts, but there is some doubt about the accuracy of these records; certainly some Green Turtles found in that area in recent years were escapes from captivity, bearing lead tags upon their flippers.

It must be admitted, however, that there is no absolute certainty that Kemp's Loggerhead is confined to the American coast. The species has been frequently confused with the Atlantic Loggerhead and it is possible that the West African records of *Caretta olivacea* Eschscholz (Boettger, 1888; Mertens, 1938), otherwise only known from the Pacific and Indian Oceans, are based upon specimens of *C. kempi*. Until a good deal more work has been done to clarify the taxonomy of the marine chelonians and to gather accurate data concerning their distribution no trustworthy deductions can be made from existing records.

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AN ANT-LIKE SPIDER FROM BRITISH GUIANA.

By Mr. R. J. WHITTICK.

(Communicated by the ZOOLOGICAL SECRETARY.)

A SPECIMEN of the Ant-like spider *Aphantochilus rogersi* Cambr. was shown beside ants of the species *Cephalotes atratus* Linn. There is a close resemblance between the spider and the ants, and they were found in association by Dr. Smart and Dr. Richards in British Guiana.

A LARVAL TREMATODE ('DIPLOSTOMUM VOLVENS') IN THE LENS OF THE EYE OF A RAINBOW TROUT.

By Dr. H. A. BAYLIS, F.L.S.

THE specimen exhibited is the lens of the eye of a Rainbow Trout, showing a heavy infestation with a larval Trematode known as '*Diplostomum volvens*'. This worm occurs in many species of freshwater fishes, and always has this peculiar habitat. It is the larval form of *Diplostomum spathaceum* (often called *Hemistomum spathaceum*), the adult of which inhabits the intestine of fish-eating birds, chiefly Gulls. The first host is a snail (*Limnaea stagnalis* or one of several other species of *Limnaea*). The fork-tailed cercaria which emerges from the snail penetrates into a fish and migrates to the eye. Epidemics have been observed in which numbers of fish have died as the result of heavy infection. This has been attributed to cerebral haemorrhages caused by the migrating cercariae. Fishes that are not killed may be rendered partially or totally blind, and this probably favours the completion of the life-cycle of the worm by making the fish an easier prey to birds.

LUMINOUS ORGANS OF SHRIMPS AND PRAWNS.

By Mr. R. DENNELL,

Imperial College of Science, South Kensington.

(Communicated by Mr. H. R. HEWER, F.L.S.)

A NUMBER of preparations of luminous organs found in certain shrimps and prawns, mainly from the *Discovery* Expedition, was exhibited.

The organs shown were of three main types. Those of the Hoplophoridae, illustrated by organs from the pleopods of *Hoplophorus grimaldii* and *Systellaspis affinis*, and from the bases of the uropods of *S. affinis*, possess a lens composed of several layers, derived from the integument, behind which are the long photogenic cells, enclosed in a fibrous theca.

The organs are innervated directly from the nerve-cord, and possess muscles by which a certain amount of movement of the whole structure is effected.

The second type of luminous organ, from the maxilla of a new species of *Sergestes*, is without a lens, and is composed of a fibrous mass enclosing clear spaces within which are rod-like bodies standing perpendicularly to the surface of the integument, and of doubtful origin. No nerve is associated with this organ.

Thirdly, preparations showing the structure of the luminous liver (organs of Pesta) of *Sergestes corniculum* were exhibited. These luminous organs are of interest in being of endodermal origin, and are composed of numbers of liver tubules, grouped in compact masses, and differing markedly from the structure of the normal liver. No lens is present, and *S. corniculum* possesses ten groups of these luminous liver tubules.

In addition, a section showing the photophore from the branchial chamber of *S. corniculum* was on view. This is a strip of tissue situated longitudinally in the roof of the branchial chamber, throwing its light downwards on to the gills.

These and other luminous organs will be described and illustrated in detail in a forthcoming paper.

THE ARCTIC ELEMENT IN THE BRITISH FLORA.

BY Dr. NICHOLAS POLUNIN,
Herbarium, Department of Botany, Oxford.

(Communicated by Prof. T. G. B. OSBORN, F.L.S.)

THE exhibit consisted of specimens of British vascular plants collected by the exhibitor in Spitsbergen, Ellesmere, and other high-arctic lands. Altogether, 57 species or geographical varieties of vascular plants in the British Flora are now known to persist north of the 75th parallel of latitude and hence to be truly arctic. All are perennials, and many reproduce chiefly by vegetative means. Classification of these plants according to their most characteristic habitat in Britain, which is almost always comparable if not identical with that occupied in the Far North, gives the following categories and figures:—

1. *Open soil or rock crevices*—competition generally negligible.
 - (a) General arctic distribution including high latitudes (c. 80° N.). 23 species, e.g. *Saxifraga oppositifolia* Linn.
 - (b) Fairly wide arctic distribution (e.g. N. Greenland and Spitsbergen). 12 species, e.g. *Salix herbacea* Linn.—total 35.

- (c) Extending far north only in Spitsbergen—tempered by Gulf Stream, 5 species, e.g. *Deschampsia alpina* (Linn.) Roem. & Schult.—total 40.
2. *Seashore and strand*—community open, competition again at a minimum.
4 species, e.g. *Carex maritima* Gunn. (*C. incurva* Lightf.)—total 44.
3. *Characteristic of other habitats* but frequently found in open areas.
7 species, e.g. *Carex aquatilis* Wahlenb. var. *stans* (Drej.) Boott—total 51.
4. *Bog or heath*.
6 species, e.g. *Vaccinium uliginosum* Linn. var. *alpinum* Bigel. (subsp. *microphyllum* Lange)—total 57.

The more significant conclusions to be drawn from these statistics are as follows: an overwhelming majority of the British vascular plants which reach high latitudes grow chiefly in the absence of competition, both towards their northern limit where the vegetation is generally open and towards their southern limit where under natural conditions it is almost always closed. No less than 44 (77.2 per cent.) are plants predominantly of open soil (or rock crevices, which are ecologically similar in that competition is generally lacking), another seven being frequently found in such situations both in the north and in the south (total 89.6 per cent.).

It may accordingly be said that truly arctic phanerogams are usually perennial dwarfs which can propagate vegetatively or flower and ripen seed in a short cool summer and endure cold and rapid changes in water-relationships, but are unable to withstand competition. They flourish in the Far North where the communities are generally open; to the south they rather naturally persist chiefly where conditions prevent the growth of ranker dominants, and where the growing season is not too long and warm for their normal metabolism. Thus in Britain the majority are rare alpine or rock crevice or other 'open' habitats.

OBSERVATIONS ON SOME SOUTH AFRICAN SPECIES OF THE GENUS *ARISTIDA* LINN.

By Mr. A. H. BUNTING.

(Communicated by Prof. T. G. B. OSBORN, F.L.S.)

DURING 1936 and 1937 I was enabled by the kindness of Prof. John Phillips and with the aid of the Botanical Survey of the Union of South Africa to carry out an ecological and systematic survey in herbarium and field of the species of

Aristida occurring in the Transvaal and in contiguous areas of other provinces of South Africa. Twenty species in all were encountered in several hundred collections, and it is possible that some points of general as opposed to local importance may prove interesting.

Ecologically, the species may be divided into two groups which have no relation to the systematic divisions of the genus. The members of the first group are confined in the area studied to primary sites, and in the majority of cases are inhabitants of very arid rocky or sandy priseral situations, although one or two (*A. Welwitschii* Rendle, *A. meridionalis* Henrard, and *A. sericans* Hack.) live in moist areas such as marshes or stream-banks.

The members of the second group have extended their range to include early secondary sites, that is, sites of recent overgrazing, ploughing, or other unnatural disturbance. Since it is clear that all secondary species must have primary homes, it was an object of my field-surveys to discover primary occurrences of such species, but certain of them were never found on primary sites in the area.

Early secondary sites in this area are characterized by an exceedingly dry soil: it is therefore interesting to observe that the hygrophilous species have never spread to secondary areas.

Further information of ecological interest was provided by a study of germination-characteristics of a few species. It was shown that the species which are confined to primary sites have always a much longer average time of germination than species which have spread to secondary sites. Since rapidity of establishment is a fundamental necessity for any secondary pioneer, this result was in accordance with expectations. Also the only really high percentage germination recorded was in *A. congesta* Roem. & Schult. (66 per cent.)—a very characteristic and frequent secondary pioneer.

The question of specificity raised several points of interest. Thus *A. junciformis* Trin. & Rupr., which in the opinion of Dr. Schweickerdt, who has recently completed at Kew a revision of the South African *Aristidas*, is conspecific with *A. Welwitschii* Rendle, is held by the writer to be distinct. The two forms, although tending to identity in their spikelet characters, are recognizably different in the field due to general differences in the shape of the panicle. Further *A. junciformis* is characteristic of secondary sites in Natal, while *A. Welwitschii* is almost rigidly confined to primary sites (hydroseral or lithoser al) on the internal plateau of the Orange Free State and Transvaal, beyond the Drakensberg escarpment.

An interesting position arises in the cases of *A. Burkei* Stapf and *A. diffusa* Trin. These species as described are placed

in very different sections of the genus. *A. Burkei* is a member of § *Chaetaria*, which has an unarticulated column, where a column is present at all (the column is a prolongation of the lemma which divides into the characteristic three awns), and *A. diffusa* is placed in § *Arthratherum* which has an articulation at or near the base of the column. Now the present collections included forms which were entirely undistinguishable in the field and occupied identical ecological positions; the specimens on examination appeared to be divided between the two species. In all characteristics except that of the articulation the spikelets were identical, and the separation became even more obviously artificial when spikelets from the same plant and even from the same panicle were found to differ in this respect. Observations on a large number of spikelets of various ages and conditions indicated that the formation of articular tissue commenced at a single point, from which it spread round the column until a complete ring was formed. This process might be interrupted at any stage by the induration of the tissues, and so all stages were found between complete articulation (*A. diffusa*) and no articulation at all (*A. Burkei*). Under these circumstances further separation was impossible, and the name *A. diffusa*, which has priority, was applied to all forms. Dr. Schweickerdt has reduced *A. Burkei* to the rank of a variety based not on articulation characters but on the geographical distribution of a particular growth-form.

Further confusion exists in the cases of *A. barbicollis* Trin. & Rupr. and *A. congesta* Roem. & Schult., which as described differ only in the shape of the panicle. This in *A. barbicollis* is open and branched, with fascicles of spikelets at the ends of the branches, while in *A. congesta* it is contracted into a false spike. A complete range of forms exists between these two extremes, and Dr. Schweickerdt has therefore concluded that they are conspecific. Field experience, however, shows that in the vast majority of cases individual plants belong clearly either to the one or to the other species, and that transitional forms are almost negligible in number. For this reason the separation of the two species should be upheld. It is, of course, possible that future hybridization or variation will continually add to the intermediate group and that ultimately a single mixed species may be produced.

One other point worthy of mention is that *A. sericans* Hack. has been rediscovered. This anomalous species, unreported ever since its first collection about sixty years ago, has been found in local abundance on the banks of the Vaal River in the Standerton district.

MARINE ALGAE FROM SOUTH AFRICA.

By Miss M. T. MARTIN, Ph.D., F.L.S., Westfield College.

THE marine algae shown were some of those collected between July and December, 1938, from different localities on the South African coast. In general, forms were selected which showed some particularly interesting problem in their structure or life-cycle, e.g. :—

(1) A number of interesting members of the Nemalionales, including :—

Nemalion furcellatum Reinbold, an alga of rare and sporadic occurrence on the shores of the Cape Peninsula. Until now, fertile specimens of this species have not been seen ; a preliminary examination, however, indicates that the structure is not that of a *Nemalion*, and this form will probably have to be transferred to another genus.

Helminthocladia Papenfussii, recently named by Kylin (1938), the structure and development of which have not yet been described in any detail.

(2) *Plocamium corallorhiza* (Turn.) Harv., a species widely distributed along the south coast. Tetrasporic and sexual plants are abundant in spring, with reproductive organs borne on the special branches, or ' stichidia ', characteristic of the genus. These are aggregated in sori, and a peculiarity is found in the proliferation of the central tissue of the sorus to form a stalked body which bears reproductive organs of a different sex or phase. Thus female plants may bear tetrasporangial sori in this way ; tetrasporic plants may bear cystocarps, and male plants mixed sori containing both tetrasporangia and cystocarps. This condition seems to arise quite commonly in mature plants, and its further investigation should be full of interest.

(3) *Gymnogongrus*, of which there are at least six species around the shores of the Cape Peninsula, of especial interest in the light of recent work on northern species of the genus. In *G. capensis* (Ag.) J. Ag., both tetrasporic and sexual plants are known, and the life-cycle would appear to be a normal one, as in the northern *G. norvegicus* ; in other species, however, e.g. *G. dilatatus* (Turn.) J. Ag., only plants bearing tetrasporic pustules are known, and, although no evidence from the development of these is yet available, the condition is very suggestive of the shortened life-cycle seen in *G. Griffithsiae*.

DEVELOPMENT OF THE ENDOSPERM IN CALCEOLARIA LINN.

By Mr K. V. SRINATH.

(Communicated by Prof. R. R. GATES, F.R.S., F.L.S.)

THE primary endosperm nucleus divides soon after fertilization and a row of three cells is organized in the embryo-sac. The middle cell, by a series of divisions, forms the nutritive endosperm. The two terminal cells divide once longitudinally and are later transformed into the prominent haustoria at either end of the embryo-sac. The developing embryo lies embedded in the central mass of endosperm cells. The contents of all the cells outside the wall of the embryo-sac are absorbed by the two terminal haustoria and transferred to the developing embryo.

PHOTOGRAPHS ILLUSTRATING THE TYPES OF VEGETATION TO BE FOUND ON ENGLISH SALT MARSHES.

By Dr. V. J. CHAPMAN, F.L.S.

Photographs of British Salt Marshes. These photographs illustrated the division of the English salt marshes into three groups, those of the south coast, those of the east coast, and those of the west coast, including marshes in Moray Firth. The south coast marshes are characterized by an abundance of *Spartina*, principally *S. Townsendii*, whilst the mud is very soft. Those marshes on the east coast also have a soft mud on the lower marshes, but the upper marshes are firmer. The vegetation is much less uniform in appearance and there is a wealth of Sea lavender (*Limonium* and *Statice*). These marshes are also characterized by a wealth of algae, including many marsh fucoids. The marshes of the west coast and Morayshire are primarily built on sand and there is a relatively low proportion of mud in the soil. The great abundance of *Puccinellia* (*Glyceria*) *maritima* is probably to be associated with their sandy nature. Another feature of these marshes is the erosion cliffs which often result in two or three terraces being found on a single marsh. It would seem that these cliffs mark periods of erosion and they are to be associated with past movements of the principal channel or channels.

A FRUITING HALIMEDA.

By Dr. V. J. CHAPMAN, F.L.S.

A FRUITING *Halimeda* was exhibited in order to call attention once more to certain similarities between the Codiaceae and the fossil Nematophytales (including the two genera *Nemato-phyton* and *Nematothallus*). Especial points of interest are

(1) The cuticle of the Nematophytales and the cuticle that can be obtained from *Halimeda*. (2) There are large and small tubes composing the thallus of *Halimeda*, and there are large and small tubes in the Nematophytales, although the arrangement in the two cases is somewhat different. (3) The sporangia in *Halimeda* are borne superficially on the expanded lobes and the spores of *Nematothallus* were also apparently borne in expanded leaf-like organs. The resemblance here, however, is not close.

The exhibit, however, did not imply that there was a definite relationship between these two groups; it simply showed that these features are perhaps suggestive in considering phylogenetic relations.

VARIATION IN RIBBING IN THE SEEDS OF TAXUS.

By Mr. M. B. ELLIS.

(Communicated by Dr. B. BARNES, F.L.S.)

ONE thousand and fifty-four seeds were collected from a single tree at Fernhurst in Sussex by Dr. Barnes in September 1936. Of these, 668 were two-ribbed, 302 three-ribbed, 76 four-ribbed, and four five-ribbed; the four remaining seeds were of the two-ribbed class, but each bore a few small additional ridges. Most of the seeds were borne singly on the twigs, but the collection included thirty-six pairs. Every pair included one two-ribbed seed, but in five of the pairs the other seed was three-ribbed, and in one it was four-ribbed.

Some study has been made of the variation shown in this large gathering of seeds. Apart from differences in size, the two-angled seeds were all similar. The three-angled seeds, however, showed much variation in the angles between the lines passing through the apices of the ridges. These angles were measured from impressions taken from the tops of the seeds. The results were shown graphically, the lowest angle being always plotted against the one nearest 60° . In more than half the seeds all three angles were found to lie between 50° and 70° .

The ribs correspond in position with the vascular supply bundles. In specimens with the arils removed the foramina for the passage of strands through the testa are clearly visible in the small, slightly sunken basal discs.

NOTHOLIRION THOMSONIANUM.

By Mr. A. D. COTTON, O.B.E., F.L.S.

A FLOWERING specimen in the living state of *Notholirion Thomsonianum*, a representative of a small liliaceous genus

from the Himalayan region, was exhibited. The species of the genus had been placed in *Lilium* or *Fritillaria*, though in either they were clearly anomalous. They differ from those of *Lilium* in the plants being monocarpic, in the tunicate bulbs with a scarious envelope (the bases of old leaves), in the long cauline leaves, in the presence of a rosette of very long basal leaves, in the 3-fid stigma (not lobed or capitate), and in the tendency for the flower to be zygomorphic. Another striking feature is the production of bulbils from the bulb-scales, which is not found in *Lilium*.

The structure of the bulb has been described by Duchartre, but the remarkable method of bulbil-formation has not hitherto been fully explained. The bulbils are not produced as axillary structures as is usually the case, but arise at varying levels on the inner face of the fleshy scales of the bulb. They appear as small swellings and invariably over a vein, but their origin is superficial and not endogenous. By a process yet to be investigated the bulbils become attached to the vascular tissue of the veins. The scales function for one year only and when the soft tissues decay in early summer the vascular tissue persists and it is these persistent veins which form the strands by which the bulbils remain for a time attached to the old scales. The 'stalk' of a bulbil is therefore not part of the bulbil, but part of a different morphological structure, namely, a vascular bundle of the mother-scale. During the shrivelling of the scale at the end of the season a certain amount of nourishment is probably passed into the bulbils.

LINALOE HEARTWOOD (*BURSERA FRAGRANTISSIMA* BULLOCK).

By MR. A. A. BULLOCK.

(Communicated by Miss M. L. GREEN, F.L.S.)

THIS species, first described in the Kew Bulletin (1937, p. 454), was collected in Mexico by Mr. G. B. Hinton, who has now sent a block of heartwood obtained in a market at San Pedro, Michoacan. It is an extraordinarily odoriferous wood and is apparently valued highly in Mexico for the manufacture of ornaments, trinket-boxes, and similar small articles, but no record of the importation of the wood of this or any other species of *Bursera* into this country since 1869 has been found.

An account of the economic value of the Mexican species of *Bursera* was published in the Kew Bulletin (1936, pp. 348-349). It appears that several species yield Linaloe oil, Linaloe wood, incense, resin, etc.

Indeed, the wood of most species is more or less fragrant owing to the presence of oil, the production of which is accelerated by injury or decay.

The highest grade of the oil is produced by a very crude, wasteful method. Trees forty to sixty years old are felled and the oil is extracted by boiling in water. The oil separated by subsequent distillation is adulterated with oil of a poorer quality extracted from the drupe-valves. The trade readily absorbs all produced, and it is, apparently, some years since any reached the London market. An attempt has been made to produce it on a commercial scale in India, but information as to its success or otherwise is not available. A sample from India was examined at the Imperial Institute in 1931, and found to be of good quality.

The resin is used in the preparation of ointments, lithographic inks, and for varnishes of excellent quality. The value of various species of *Bursera* is stressed in all Mexican works on *materia medica*, particularly in the treatment of uterine diseases.

SOME ANNOTATIONS IN LINNAEUS'S BOOKS SHOWING HIS GEOGRAPHICAL INTERESTS.

By Mr. S. SAVAGE, F.L.S.

HAVING completed recently a catalogue of the annotations in Linnaeus's printed books, I am able to state that but relatively few notes of a purely geographical character are to be found there. Beyond a few special notes, such as one on the Nile and another on the Alps, the greater number of the notes that can be called geographical consists of habitats of plants and animals added by Linnaeus to his own works.

The habitats given in Linnaeus's works were conditioned by the information available to him at the time of writing; vague, as in *India*, in *America*, in *Oriente*, or in *Oceano*; less vague, as in *India orientali*, in *America meridionali*, in *Virginia*; more precise, as in *Angliae Devonshire*, in *agro Tingitano*, *Monspeli*. In some cases he added the collectors' names as if vouching for the habitats; in others he added some author's name as a book authority, as in *Graecia Wheeler*. Generally speaking, his main concern was with the systematic treatment of the plants and animals.

A geographical error made by Linnaeus concerning Mutis's plants was the occasion of the following passage in Sir James Edward Smith's 'A selection of the correspondence of Linnaeus . . .', London, 1821, ii. p. 508:—'He (Smith) finds in the old Dutch Atlas of Frederick de Wit, which Linnaeus always used, the name of New Granada applied to New Mexico.'

the principal town of which is Santa Fé, in latitude 39 north. This Linnaeus undoubtedly took for the residence of Mutis; the real New Granada, with its capital Santa Fé de Bogotá, lat. 2 north, being so much less conspicuous in the same map as to have escaped observation.' It is a matter for regret that Linnaeus's atlas did not reach the Society with the Linnaean Collections; it being retained by Lady Smith as a non-scientific book. There are several editions of de Wit's Atlas, which is fol. max. in size and consists of copper-plate engravings.

An instance of Linnaeus's persistence in obtaining more precise information of a small locality was the subject of the exhibit. The region north of Montpellier was of special interest to Linnaeus because several of the earlier botanists knew it well and had collected there. On the fly-leaf of his copy of Magnol's '*Botanicum Monspelicense*', 1688, he noted information about the localities known as Hortus Dei, Mons Ceti, etc. In the Linnaean thesis, '*Flora Monspelensis*', 1756, these and other pieces of geographical information were printed; and in the annotated copy of this thesis exhibited there are many corrections to them in Linnaeus's handwriting. Linnaeus was much interested in the locality known as Hortus Dei, situated about 12 leagues to the north of Montpellier; and wrote a MS., '*Iter ad Hortum Dei*', which is as yet unpublished. The place-name Hortus Dei occurs in the writings of Caspar Bauhin, Burser, Ray, Tournefort, and others; and is to be found on Cassini's map of France as Hort de Dieu. Many of the letters in the lengthy correspondence between Linnaeus and Professor François Boissier de la Croix de Sauvages, of Montpellier, discuss the plants found in the districts around Montpellier; and Linnaeus obtained from that valued correspondent much precise information concerning both plants and habitats. In the exhibit this imaginary journey to Hortus Dei could be followed in part on Cassini's map of the district, dated 1744. I am indebted to Mr. F. Allen, Map Curator to the Royal Geographical Society, for the selection and the loan of the sheet of Cassini's map.

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